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MULTIPLE ALLELOMORPHS IN MICE

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SOME breeding experiments with mice that I have been carrying on during the last two years have shown that yellow, gray gray-belly, gray white-belly and black are allelomorphs. To this series a fifth allelomorph may possibly be added which for the present may be called new gray. This quadruple (or quintuple) system of allelomorphs fulfils the conditions of a multiple series in that only two of the allelomorphs can exist at the same time in any individual. In other words, a mouse may be pure for any of these genes (except for yellow, in which the pure form is not viable), or a mouse may be heterozygous in any two of the genes, but never in more than two. The evidence that establishes this series of allelomorphs may be briefly stated as follows:

In 1911, I pointed out that if yellow mice (producing yellow and chocolates) are bred to agoutis (grays), and their yellow offspring mated, they should produce not only yellow and agoutis (as they did) but some chocolates (or blacks) also; but no chocolates appeared. I stated that the results obtained were explicable if yellow and agouti are allelomorphs.[1]

[1] The discussion in the same paper of the presence of chocolate yellow and black bars in the ticked hair in relation to the occurrence of chocolate, yellow and black color in domesticated races may only confuse the ontogenetic production of characters with the gametic inheritance of factors. The

Sturtevant (1912) showed that the results are also consistent with the hypothesis that there is close or complete linkage (genetic coupling) between yellow and agouti. In principle this is the same as saying that when yellow and agouti enter from different sides (mother and father) they separate in gametogenesis, or in other words they "repel" each other and behave, as I said, like allelomorphs.

The numerical results would be the same whether yellow and agouti are treated as though completely linked or whether they are treated as allelomorphic. What I had vaguely seen in my 1911 paper was clearly explained in the following year by Sturtevant's treatment of the same data, to which he added that of Little and Miss Durham.

Sturtevant showed, from an analysis of Miss Durham's results, in which she used ordinary gray (gray "gray-belly") mice, that her results are consistent with the hypothesis of absolute linkage, or, on my interpretation, with the hypothesis of allelomorphism. Sturtevant's conclusions were promptly contradicted by C. C. Little on the evidence furnished by some of his earlier experiments, in which he obtained yellow, grays and black (or chocolates) in offspring from yellow to black (or chocolates). Such a result would be inconsistent with Sturtevant's hypothesis. Little also appealed to certain experiments of Miss Durham, in which, he stated, results like his own are given. Since Little has been unable to get again his former results, but has obtained evidence in favor of Sturtevant's view, and since it is clear that he misunderstood Miss Durham's evidence, his contradiction ceases to have any weight.

factorial hypothesis relates to those differentials that serve to separate different types in inheritance and is not concerned with the problem as to how those differentials produce their effects. Breeding experiments show that gray differs from black by one differential, from yellow by another, and from cinnamon by a third. So far as Mendelian segregation of these differential genes is concerned it is of no consequence that the gray hair is made up of a black, a yellow, and a chocolate band.

After the publication of my own and of Sturtevant's paper I set to work to obtain crucial evidence in favor of, or opposed to, the view that yellow and gray are allelomorphic. Little, also, it appears, has carried out some new experiments which he has recently published, with the results just stated. My own data have been ready for some time, but I have withheld them in order to get a sufficient body of evidence to make the case convincing, especially in the light of the possibility that the crossing over might occur in one sex and not in the other. For, if no crossing over occurred in the male, there might be crossing over in the other sex, which would not reveal itself unless the experiments were deliberately planned so that both sexes are tested. This consideration seems to have been overlooked by Little, for he has omitted in his confirmatory paper to give the sexes of the animals used. Without a knowledge of this relation even his confirmation fails to confirm (as he supposes) the view that he formerly combated.

Since Miss Durham worked with common gray and I with gray white-belly, and both are "repelled" by yellow, *i. e.*, both are allelomorphs of yellow, it follows that these two grays are also allelomorphic to each other.

The evidence that black belongs to the same series of allelomorphs is obtained in the following way: If a given yellow is mated to black, and yellow and gray offspring are obtained, and if then the yellow offspring are mated to black again and now give yellow and black only, the proof is furnished; for in the first mating yellow and agouti have repelled each other, and the yellow-bearing gametes have united with the black gametes of the other sex to give the yellow offspring. The second mating shows that black is now repelled in turn by yellow and is therefore allelomorphic.

This may be illustrated in the following way: Let B^Y = yellow, b = black and B = gray. These three factors may be treated as allelomorphs, then:

Yellow $B^{Y}B$ by black bb.

Gametes of P_1 yellow B^{Y}–B.
Gametes of P_1 black b–b.

F_1 $B^{Y}b$ = yellow.
Bb = gray.

Gametes of F_1 yellow B^{Y}–b.
Gametes of pure black b–b.

F_2 $B^{Y}b$ = yellow.
bb = black.

But if yellow and black and gray are not allelomorphic the same matings should give the following results:

Y' = yellow. y' = not yellow. b = black. B = "gray" (not black).

Yellow $Y'y'BB$ by black $y'y'bb$.

Gametes of P_1 yellow $Y'B$–$y'B$.
Gametes of P_1 pure black $y'b$–$y'b$.

F_1 $Y'B$ $y'b$ = yellow.
$y'B$ $y'b$ = gray.

Gametes of F_1 yellow $Y'b$–$Y'B$–$y'b$–$y'B$.
Gametes of pure black $y'b$–$y'b$.

F_2 $Y'b$ $y'b$ = yellow.
$Y'B$ $y'b$ = yellow.
$y'b$ $y'b$ = black.
$y'B$ $y'b$ = gray.

On the second assumption yellow, gray and black should appear in the back cross. The former and not the latter view is therefore consistent with the actual results.

THE SYMBOLS EMPLOYED

It is, of course, a matter of secondary importance what system of symbols is followed. The requirements are simplicity, consistency and suggestiveness, but one can not always arrange to have all three at the same time. The simplest scheme, for a system of allelomorphs like these, would be to have some common letter to indicate their relation and an exponent to suggest the different characters for which each stands. If we take the symbol b (black) for the common letter, and use capitals for dominance, the allelomorphs will be:

b = black.
B^{G} = gray gray belly.
B^{W} = gray white belly.
B^{Y} = yellow.

If one preferred to take Y (yellow) as the common letter the series would be y'^{b}, y'^{g}, y'^{W}, Y'; or, if one preferred

to take G (gray), as the common letter, the series would be g^b, g^W, G, g^Y. On the whole the first series seems to me somewhat preferable.

The factor for cinnamon is entirely independent in heredity of the preceding series of allelomorphs. This factor may be represented by *ci* and its normal allelomorph by *Ci*. The formula for the wild gray would then be *Ci Ci*, and that for cinnamon would be *ci ci*. Black would be *b b*, and the double recessive cinnamon black (or chocolate) would be *bb ci ci*. Chocolate is one of the commonest types of domesticated mice and since I have used it very extensively in my matings, its relation to the other types may be further stated. It is known that if chocolate is bred to wild gray, and if the gray offspring that are obtained are then inbred, they give, in F_2, the following classes: 9 wild gray, 3 cinnamon, 3 black, 1 chocolate.

It is clear that chocolate is the double recessive type. Of the two genes, that differentiate chocolate from wild gray, chocolate has one in common with cinnamon and the other with black. In other words, chocolate is cinnamon black, and technically should receive this name.

The Experimental Evidence

Is There a Separate Factor for White-belly?

The first series of experiments was made in order to determine whether the peculiarity of white-belly, shown by the wild race of white-bellied grays, is due to a factor that may be separated from the gray white-bellied mice, or whether it is completely linked to gray (or allelomorphic to it). As wild gray house mice offer some drawbacks in breeding work, I used cinnamon blacks (chocolates). Gray white-bellied mice were bred to

[2] It is not possible to make a system of allelomorphs (in which the "compounds" are serially epistate to each other) consistent entirely with the system of nomenclature that I have suggested for the usual cases in which mutant allelomorphs are contrasted with the normal allelomorphs of the wild (or supposed original) type.

chocolates.[3] The gray white-bellied offspring were selected and these were bred again to chocolate. The cross, in regard to sex, was made both ways. If there is an independent factor for white-belly that can separate from the factor for gray gray-belly, then some gray gray-bellied mice should appear. None were obtained, as the following table shows. We must conclude either that there is one factor that gives the gray white-bellied coat, or else that the postulated factor for white-belly is so closely linked to the gray factor that it has not separated once in 100 times. Therefore unless such a separation occurs it is simpler to assume one factor for gray white-belly that is allelomorphic to black and to gray gray-belly, etc.

TABLE I

Mating	Gray or Cinnamon White-belly		Black		Chocolate		White	
	♂	♀	♂	♀	♂	♀	♂	♀
Gwb ♀ by Ch ♂....	7	21	2	9	5	11	3	1
Ch ♀ by Gwb ♂....	2	14	3	10	4	10		
Totals.....	9	35	5	19	9	21	3	1

Taking both crosses together, there are 44 grays to 54 blacks and chocolates, which approximate at least to expectation. To these numbers I may add the following data taken from similar experiments made for other purposes in which one parent was, as before, gray white-belly.

Gray-white Belly.		Black or Chocolate.	
♂	♀	♂	♀
17	25	20	20

Presumably, therefore, the results may be treated as though a single gene for gray white-belly exists. It will be observed that the experiment has been made in two ways, for at the time I was aware of the possibility that crossing over, if it occured, might be limited to one sex.

[3] At the time when the experiment was made all the gray white-bellied mice were heterozygous for black and for agouti (including some with the factor for cinnamon).

We are justified, therefore, in treating gray white-belly as an allelomorph of gray gray-belly, the former dominating. If crossing over should occur, it might perhaps only be realized in the gray or cinnamon mice, since it is possible that the ticked condition of the hair (that is, common to gray and to cinnamon) is necessary to realize this condition. The expected crossover that would be observed would be gray gray-belly mice. The contrary class would then be black or chocolate mice that carry the factor for white-belly that might or might not show the influence of the supposedly separable factor.

My white-bellied stock of mice had been killed after my earlier results had been published, but Mr. B. B. Horton had kept some of my original stock alive, and from him I obtained a few of these mice in 1912 to carry on the above experiments.

An extraordinary sex ratio appears in the next to the last table, where there were 26 males to 76 females, approximately 1:3. The mice were entered when about three weeks old. The sex was noted, but no special attention given to the determination. There is some chance of mistaking the sex of young mice, but one familiar with these animals can determine with certainty the sex at three weeks if sufficient care is taken. I have no reason to suppose that I made such errors which would have to be frequent to give these results. If taken, then, at their face value, the data seem to show that there is a sex-linked lethal gene present here. It is not linked to any of the factors involved, and this is not expected, since neither black nor agouti is sex-linked. If further work confirms this conclusion (and I hold it as a provisional conclusion until it can be further studied) we have here the first evidence of a sex-linked gene in mice. A sex-linked lethal should give a sex ratio of 1♂:2♀.

The Allelomorphism of Yellow, Gray and Black

The allelomorphism or "repulsion" of yellow and agouti (gray) may be tested in various ways. One of the

simplest tests is the following: Yellows were bred to chocolates. The combination gave yellow and agouti offspring, when certain yellows are used, and yellow and chocolate offspring when other yellows are used. Mixed litters of yellow, agouti and chocolate do not appear. Now when yellow and agouti appear in a given litter (as above) the yellow parent must have carried agouti. If her yellow gene "repels" the agouti gene, then none of the yellow daughters should contain agouti genes, consequently if such yellows are next bred to chocolate the offspring should be only yellow and chocolate (or black) and never yellow and agouti. This, in fact, is what my experiments have shown. In the two following tables the results of crossing yellows by chocolates are given by litters. The yellows that were used at first were for the most part heterozygous for gray white-belly, hence in the earlier litters yellows and grays were generally obtained. The yellow offspring of these earlier litters were for the most part used in the later experiments, hence the later litters are made up of yellows and chocolates. The records (not given here) showed in every case that yellow mice from litters of yellow and gray gave, when bred to chocolate, only yellows and chocolates.

TABLE II

YELLOW ♂ BY CHOCOLATE ♀

LITTERS

Yellow	1	1	1	4	3	1	3	2	4	4	9[4]	4	4	2	5	5	4	3	5	7	2	2	2	2	3	4	3	2	4	1	2	2	2
Gray	.	2	.	5	4	2	2	.	.	4	4	5	5	.	.	3	4	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.
Chocolate	.	.	1	.	.	.	.	.	4	.	.	.	.	4	.	.	.	2	3	4	3	.	3	3	.	2	3	2	.	3	4	2	3
White	1	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE III

YELLOW ♀ BY CHOCOLATE ♂

LITTERS

Yellow	4	1	4	4	3	4	4	2	4	1	4	8	8	1	2	2	8	3	2	2	1	1	4	3	4
Gray	5	.	2	5	2	1	1	2	.	3	5	1	3	1	.	.	3	.	.	.	.	.	.	.	.
Chocolate	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	2	.	1	.	2	3	4	2	3	1
Black	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
White	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.

[4] Probably two litters combined.

TABLE IV

SUMMARY OF LITTERS

Yellow and Gray		Yellow and Chocolate	
Yel.	Gray	Yel.	Choc.
101	78	70	67

The experiment is not demonstrative, however, unless both the yellow daughters and sons are bred to chocolate, for it might be that yellow and agouti are linked and crossing over might occur in one sex and not in the other sex. For instance, if we start again with yellow by chocolate, then if their yellow offspring contain agouti linked to yellow that does not cross over in one sex, let us say in the males, it follows that a yellow male bred to chocolate would give only yellows and chocolates, for the agouti gene would go with the yellow. Therefore, both sexes must be tested. This essential element in the proof has been overlooked by Little, for he fails to state whether his test experiments were made with both sexes. In my main experiments I have used yellow sons only, and the tables are based on those data, but in a few cases I have mated the yellow daughters (whose brothers were agouti) also to chocolate and have found that these females give only yellows and chocolates, which shows for both sexes that no crossing over of yellow and agouti occurs.

A specific case will illustrate this point. A yellow male was bred to a chocolate female and gave 5 yellow and 7 gray offspring in two litters. One of the yellow daughters was bred to chocolate and in four litters produced 11 yellows and 9 chocolates. A yellow granddaughter gave 9 yellows, 7 chocolates and 4 whites.

A yellow female bred to chocolate gave 8 yellows and 16 chocolates, but as I have no record of the preceding generation, I can not be sure that this result is comparable to the last. It shows at least that a yellow female gave only two kinds of offspring.

A "NEW GRAY" FACTOR

A word may be added about the "new gray." In the original stock obtained from Mr. Horton there was a

gray female with a not-pure-white belly. She was not used in the main lines of the experiments described above. But she was kept in stock and bred with chocolates. About a year later I noticed in the offspring of a pair of cinnamon white-bellied mice a few mice that looked like chocolates, but which showed, on closer inspection, distinctly ticked hair. One of these new grays bred to black (heterozygous) gave some chocolates, blacks, new grays, and one very dark, almost black, mouse with ticked hair.[5] The female was bred next time to a house mouse (gray gray-belly) and produced all gray gray-bellied offspring that had a dark coat, but not nearly so dark as that present when the new gray is heterozygous for black. Until further tests have been made it can not be stated whether or not the new factor belongs to the yellow-black system of quadruple allelomorphs.

[5] The resemblance of this mouse to the rabbit "agouti-black" homozygous for black is very striking (Punnett, *Jour. of Genetics*, II, 1912).

THIRTEEN YEARS OF WHEAT SELECTION

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INTRODUCTION

IN 1901 the Minnesota Agricultural Experiment Station planted a number of varieties of wheat from the *polonicum, spelta, turgidum, durum* and *vulgare* types in foundation beds in order to have specimens of these different types always on hand for class work, hybridization or demonstration purposes. Six of these varieties—hedgrow (*turgidum*), Russian (*vulgare*), common speltz (*spelta*), kamouka (*durum*), and Polish (1) and Polish (2) (varieties of *polonicum*)—have been grown continuously since that time and an effort has been made to improve them by selection. The method followed was that introduced at this station by Professor W. M. Hays and called the "centgener" method.

The centgener method consists, briefly, in starting with individual plants, planting one hundred selected kernels from each plant at equal depths and at equal distances apart in separate plots. A plot of one hundred plants is called a centgener. Careful notes are taken on the plants in each centgener and at harvest time five or more of the highest yielding plants are selected from which the seeds for planting the next year are taken. From these five best plants from five to ten of the best heads are selected and thrashed together. One hundred of the largest and plumpest kernels are then selected out of the seed obtained by thrashing these selected heads, and these are planted in the centgener test the next year. This work is continued from year to year, each season the hundred best kernels from the five or more best plants being planted in succeeding centgeners.

In 1908 an experiment was planned with the object of developing a strain of wheat which would have a minimum amount of culm exposed between the base of the spike and the upper leaf sheath, or in other words, to produce a short-necked variety of wheat. The ultimate purpose of reducing the neck lengths was to reduce the area of the stem exposed to the black stem rust. Since this rust ordinarily does little damage to that portion of the culm enclosed in the leaf sheath, it was thought that a short-necked wheat would be more likely to escape serious damage from stem rust than a long-necked kind. For this work individual plants were selected which had short necks and the seed from these were planted in separate centgeners. Each year at harvest time ten or more plants which appeared to the observer to have the shortest necks were selected from each centgener and measurements of their neck lengths were made and recorded. One hundred kernels were saved from these shortest necked plants each season for subsequent centgeners, thus making a continuous selection for short neck lengths.

The data derived from the above experiments seems to throw some light upon the much-discussed question as to whether or not selection within a pure line can increase yield or change type enough to make it a desirable practise from the practical breeder's standpoint. In both of the experiments, we have the requirements for a pure line satisfied. Wheat is a normally self-fertilized plant. Each centgener was started from a single head in 1901 and these heads have bred true to type ever since.

The long period of years over which this experiment has extended makes the data particularly valuable. One of the adverse criticisms to most pure line work is that it has not extended over a long enough period of time. Thirteen years are about as long as any practical breeder would be apt to keep up selection on one pure line and covers the longest period of continuous selection for a self-fertilized plant yet reported.

Another criticism to pure line investigations is that in

many cases it has not appeared certain that the material studied was a pure line. Since the plants have bred true to type throughout the whole period of study, it is obvious that this criticism will not hold for the data herein presented.

The work has been conducted at this station under the direction of Professor W. M. Hays from 1901 to 1905, under Professor E. C. Parker 1905 to 1908, under Professor Andrew Boss from 1908 to 1911 and under Professor C. P. Bull 1911 to 1913.

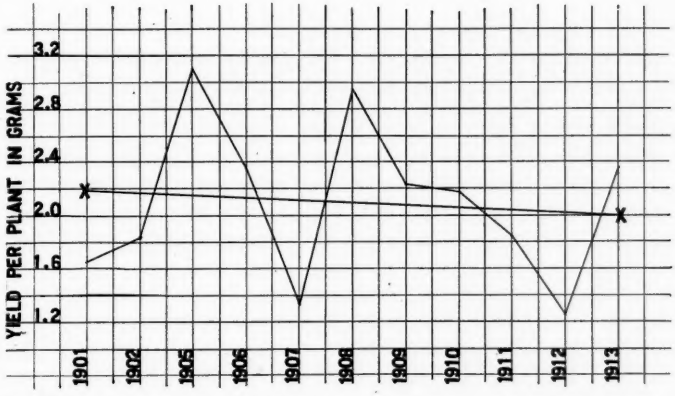

PLATE I. Average yield per plant for all varieties. X–X, fitted straight line.

SELECTION TO INCREASE YIELD

The varieties studied, the average annual yield of each variety and the average yield per plant for the six varieties under test are shown in Table I. In the years 1903 and 1904 weather conditions were unfavorable, making it impracticable to obtain correct average yields per plant, so data for these years were omitted. However, selections of the best plants were made in these two seasons as in the others and the best seed from them were kept for planting, so the continuous selection for increased yield was uninterrupted.

TABLE I

SHOWING YIELD PER PLANT—YEARS 1901–1913

Name of Variety	Yield per Plant in Grs.										
	1901	1902	1905	1906	1907	1908	1909	1910	1911	1912	1913
Hedgrow	3.10	2.80	3.69	2.48	1.27	3.75	2.49	2.55	2.02	.99	3.67
Russian	1.00	1.70	3.57	1.96	1.71	2.74	2.71	2.17	1.95	1.37	2.70
Speltz	2.40	1.80	3.99	2.99	1.38	3.38	2.40	2.86	2.01	2.14	2.59
Kamouka	1.50	2.50	1.99	2.69	1.39	3.31	2.19	2.48	1.67	1.35	2.16
Polish (1)	.80	1.30	2.52	2.04	1.03	1.48	1.91	1.70	1.56	1.12	1.74
Polish (2)	1.10	.95	2.83	1.97	1.26	....	1.61	1.31	1.78	.51	1.33
Average	1.65	1.84	3.10	2.35	1.34	2.93	2.22	2.18	1.83	1.24	2.36

SELECTION TO INCREASE HEIGHT

The average height of the plants for each year of the test is shown in Table II. Though no attempt was made to select for increased height, since a number of workers have shown that height in the small grains is distinctly correlated with yield, it is natural to suppose that the selected plants were among the tallest as well as being the highest yielders of each year's crop. When this experiment was begun, it was not known that height and yield

TABLE II

SHOWING AVERAGE HEIGHT PER PLANT—1901–1913

Name of Variety	Height in Inches									
	1901	1902	1905	1906	1908	1909	1910	1911	1912	1913
Hedgrow	36	41	42	43	46	41	38	41	36	36
Russian	34	37	40	35	44	41	33	36	35	32
Speltz	34	38	37	47	44	41	39	42	39	35
Kamouka	36	34	34	38	40	40	32	38	36	33
Polish (1)	40	38	41	38	42	42	33	39	38	33
Polish (2)	28	30	37	37	.....	35	31	38	31	32
Average	35	36	38	39	43	40	34	39	36	33

were correlated, so the figures on height were kept merely as a matter of general interest and with no idea that they would have bearing on the problem. Among those who later found height correlated with yield are Deneumostier ('10),[1] Love ('11),[2] Myers ('12),[3] Leighty ('12)[4] and

[1] Deneumostier, C., "Correlations in Wheat," *Ann. Gembloux*, 20, No. 5, 1910.

Selection to Decrease Neck-Lengths

The result of the selection for short neck-lengths is shown in Table III. This is a clear illustration of how misleading short-term experiments may be. Had the experiment been discontinued at the end of the third year, the figures would have indicated that it was possible to modify this character very rapidly by selection. However, in the following two years the neck-lengths seemed to revert to the mean of the pure lines, and the last year they were actually longer than when the experiment was started. The reduction in the first three years was probably due to growing conditions.

TABLE III

Showing Result of Selection for Short Necks

	Average Neck L ngth in Curve				
	1909	1910	1911	1912	1913
Series *A*	7.4	1.86	.24	7.34	9.54
Series *B*	6.1	1.12	.79	8.13	11.6
Series *C*	5.8	1.65	.56	7.53	8.21
Series *D*	5.2	2.08	.59	10.47	13.82

Discussion

From the data presented in these tables, it is evident that there has been no permanent gain for these thirteen years of selection either in yield per plant, height of plant, or shortening of neck-lengths. The expected seasonal variations occur. A comparison of the yield of Haynes Blue Stem, which is grown extensively in Minnesota, and was continued in the variety test without any attempt at selection throughout the whole period, with Hutcheson ('13).[5]

[2] Love, H. H., "A Study of the Large and Small Grain Question," *An. Rep. Am. Br. Asso.*, 7: 109–118, 1911.

[3] Myers, C. H., "Variation, Correlation and Inheritance of Characters of Wheat and Peas," Cornell University Thesis, 1912.

[4] Hutcheson, T. B., "Correlated Characters in *Avena sativa*, with Special Reference to Size of Seed Planted," Cornell University Thesis, 1913.

[5] Leighty, C. E., "Studies in Variation and Correlation of Oats, *Avena sativa*," Cornell University Thesis, 1912.

the average yield of the selected varieties, is shown in Table IV. The average yield in bushels of the Haynes Blue Stem is also platted in comparison with the average yield of the selected varieties in Plate II. In 1912 a severe hail storm injured the variety plats so much that

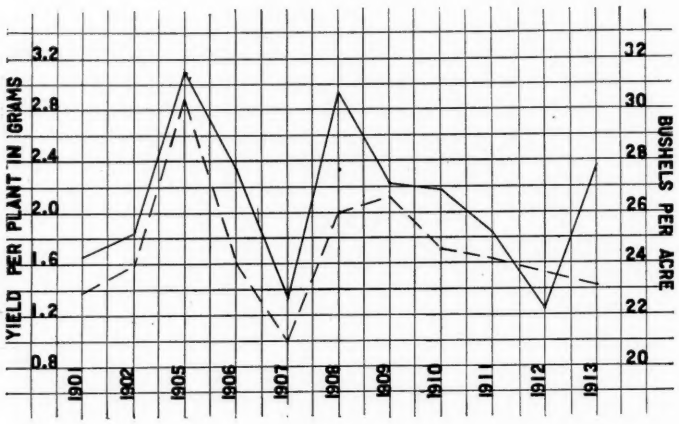

PLATE II. Comparing seasonal fluctuations in selected lines with unselected Blue Stem. Solid line, yield per plant in grams for selected lines; dashed line, yield in bushels per acre for Blue Stem.

it was thought best not to include the yield of the Haynes Blue Stem for that year. This gives an incorrect appearance to the curve, as it was extended just as if this year was present and midway between 1911 and 1913 in yield. It will be noticed from Table IV and Plate II that the

TABLE IV

COMPARING SEASONAL FLUCTUATIONS IN SELECTED LINES WITH UNSELECTED BLUE STEM

	1901	1902	1905	1906	1907	1908	1909	1910	1911	1912	1913
Yield in grs. per plant for selected lines	1.65	1.84	3.10	2.35	1.34	2.93	2.22	2.18	1.83	1.24	2.36
Yield in bu. per acre for blue stem	22.9	23.9	30.4	24.00	21.00	26.00	26.6	24.6	24.2	.....	23.2

fluctuations from year to year agree very closely. These data indicate that increased yield is due to favorable environmental factors and not to improvement by selection.

A comparison of the yield of each variety for the first five years of the test with that of the last five years is shown in Table V. The data in this table show that there is no significant difference in yield for these two periods. In Russian and Polish (1) there is a slight increase in favor of the latter period, but in the other four varieties there is just as much decrease for this period. However, there is not enough difference in any case to indicate either permanent improvement or decrease in yield. As far as these varieties are concerned, it seems that selection has brought about no permanent improvement.

TABLE V

COMPARING THE YIELD OF THE FIRST-YEAR PERIOD WITH THAT OF THE LAST FIVE-YEAR PERIOD

Name of Variety	1st 5-year Period		Last 5-year Period	
	Height	Yield	Height	Yield
Hedgrow	41.6	2.67	38.4	2.34
Russian	38.0	1.99	35.4	2.18
Speltz	40.0	2.51	39.2	2.40
Kamouka	36.4	2.01	35.8	1.97
Polish (1)	39.8	1.54	37.4	1.61
Polish (2)	33.4	1.62	33.4	1.31
Average	38.2	2.06	36.5	1.97

A curve of the yields of the six varieties under consideration for the thirteen years of the test was plotted and a straight line was fitted to it, by the method of the least squares, to indicate the trend of the yield. This curve is shown in Plate I. There is a slight downward tendency in this straight line, but it is not enough to indicate a tendency toward decrease in yield. The line fitted to the curve of height (Plate III) also shows a slight tendency downward.

The data herein cited are not sufficient for definite con-

clusions. However, the indications are that from a practical breeder's standpoint permanent improvement in pure lines in small grains, if possible, is certainly not rapid or apt to be very marked. Thirteen years of selec-

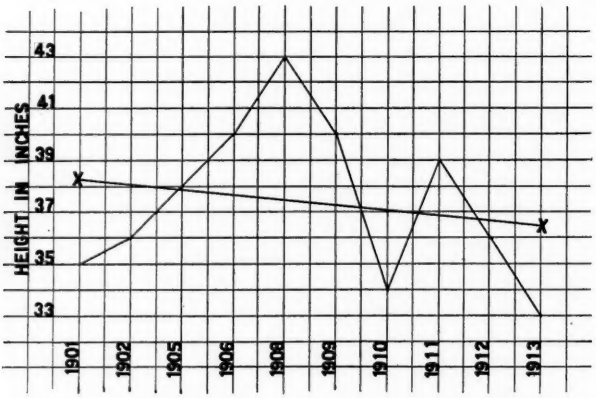

PLATE III. Average height of all varieties. X–X, fitted straight line.

tion covers considerable time and expense, and, as far as can be seen from the varieties reported in this paper, it has resulted in no permanent improvement. This would suggest that some other line of improvement must be sought. It is probable that much more rapid progress could be made by segregating pure lines from mixed populations and combining the desirable characters of these lines by hybridization.

PATTERN DEVELOPMENT IN MAMMALS AND BIRDS

II

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PARTIAL ALBINISM IN WILD MAMMALS

Partially albinistic individuals of species that normally are wholly pigmented, occur frequently in a wild state, and almost any large series of a given species may contain a few. I have examined many such, in which it was perfectly evident that the white mark was due to areal restriction of some one or more of the primary pigment areas just as described in the various domestic species. It is apparent that the white markings in both are quite comparable, but in species under domestication no agency seems present whereby such pied individuals are eliminated, whereas in a wild state the sudden acquisition of a large amount of white in an individual would not only render him too different from his fellows, but might put him at a disadvantage because of a conspicuousness to which as a species he had not yet become accustomed.

There are many other species in which, as we now see them, white markings form a permanent and normal part of the pattern. Among those in which these white markings are few or simple, it is often evident that they are merely primary breaks between the pigment patches that have become more or less fixed by long periods of selection, whether natural, sexual or otherwise. As I shall endeavor to show, there are species in which a beginning has already been made towards the development of a pied pattern, though it has not yet become well fixed. Still other species show a more complicated white and pigmented pattern, the white portions of which can not readily be derived from primary breaks alone. Such I take to be highly developed patterns and make no attempt

to analyze them here. Examples of this type are seen in the zebra, the spotted skunks (*Spilogale*), the striped weasel (*Ictonyx*). Probably more than one factor is responsible for some of the combinations of stripes and spots seen, for example, in certain spermophiles (*Citellus 13-lineatus*), but I shall not now attempt a discussion of these.

One of the most frequent manifestations of pigment reduction in mammals is the presence of a white spot in the normally pigmented forehead. This is due primarily to the reduction of the ear patches, which fail to meet at their median edges. Perhaps, too, the apparent loss of the crown patch in some mammals still further tends to lessen the amount of pigment production at this point. Rabbits and hares very often have more or less white in the forehead, but none of the species has developed this sufficiently to make it a permanent mark. Moseley in his "Naturalist on the *Challenger*," speaks of a "black variety" of wild rabbit—doubtless introduced—"with a white spot on the forehead" as occasionally found on Teneriffe, Canary Islands, but this mark is common, and I have seen it in such widely sundered species as the eastern varying hare of New Hampshire and the black-necked hare native to Java. A specimen of Leisler's bat (*Nyctalus leisleri*) in the Museum of Comparative Zoology has a white spot in the middle of the forehead and another on the mid-ventral line of the abdomen—the first a primary break between the ear centers, the second probably a ventral primary break between those of the sides. Among the Insectivora, the West Indian *Solenodon paradoxus* has a white patch at the nape of the neck which has become a permanent part of its pattern. It is clearly the enlargement of a primary break separating the ear patches and neck patches on the median dorsal line. It is a fact of much interest that in a considerable series of this species in the collection of the Museum of Comparative Zoology hardly two have it developed alike, but it varies from a few white hairs to

a large patch 15 × 10 mm. wide. Evidently it has not yet become precisely defined in its limits, though now a permanent mark of the species.

White marks in the forehead are common among the species of the Mustelidæ or weasel family. A narrow white median line is present in the Javan mydaus and in the skunks (*Mephitis*) as part of the permanent pattern.

In the badger (*Taxidea*) a white line is not only present on the forehead, but it is often extended medially so as to separate the pigment patches of both sides of the body. In the New York weasel (*Mustela noveboracensis*) of the eastern United States a few white hairs are often present on the forehead, and other instances could be multiplied. Among monkeys, a white spot on the nose is present in some species of *Lasiopyga,* and in an allied genus *Rhinostigma,* it is elongated vertically to form a white streak.

A yet more illuminating case is that of the Muskeget Beach mouse (*Microtus breweri*) a derivative of the common brown meadow mouse of the New England mainland. On this island of white sand off the Massachusetts coast, a pale variety has developed which is very distinct from that of the neighboring shores. Not only is it a paler race, but albinism also has begun to appear, so that occasional individuals have a white fleck between the ears, showing the drawing apart of the ear patches. Of a series of 62 specimens in the collections of the Museum of Comparative Zoology and the Boston Society of Natural History, no less than 13 had such white flecks, and one had in addition a white spot just in advance of the shoulders, marking the line of separation between neck and shoulder patches. In our studies on the heredity of coat colors in mice, Professor Castle and I discovered (Allen, 1904; see also Little, 1914) that the pied condition is recessive in the Mendelian sense towards the self colored, so that partial albinos bred to wholly pigmented mice produce in the second generation, if interbred, 25 per cent. of spotted young. The figures

given above (13 in 62) are near this in case of the Muskeget mouse, but the matings are of course more promiscuous. The case is interesting in connection with the studies of Ramaley (1912) and Pearl (1914), tending to show that in a mixed population the recessives may increase so as to exceed the dominants. Although the spotted mice do not, in case of this species, exceed the unspotted individuals, they nevertheless are of far more frequent occurrence than they are in the mainland representatives of the species. This accords with the fact that island-living mammals are very commonly albinistic, and the cause is doubtless that the population is much more inbred, so that the recessive condition of partial albinism is more likely to be propagated than if successive generations have a wider range over which to spread. It seems probable that heredity will tend to increase the proportion of spotted mice of Muskeget, and that if this condition is disadvantageous, a large part of the spotted individuals will be killed off, yet in the course of time they may become adjusted to this condition and will survive in increasing proportion till the white mark becomes characteristic of all the animals. Cory (1912) records the capture of seven muskrats at Hayfield, Iowa, all of which were uniformly marked, having a white ring around the neck and the entire underparts, feet, and end of tail white. I can think of three causes influencing the status of such white markings. These markings may be inherited in a purely automatic way as unit characters; but if thus inherited they may be (1) increased through selection, natural or sexual; or (2) eliminated by the same agent; or (3) they may be, at first, of no influence at all in the economy of the animal and persist or not, according as they are heritable.

I have mentioned that island mammals tend to be more albinistic than their mainland representatives. Other cases may be mentioned, as the common squirrel (*Sciurus vulgaris leucurus*) of Great Britain, which differs notably from that of the continent in having frequently a

white or whitish tip to the tail, often for one half its length. A similar white tip is occasionally seen in our red squirrel (*S. hudsonius*) as an albinistic mark, and is due, of course, to the terminal restriction of the rump patches. The deer of Whitby Island, Puget Sound, are said to be much marked with white, and sundry marsupials of Papua as well as the monotreme *Zaglossus* are subject to white markings. In the cuscus (*Pseudochirus*) the pigment is sometimes restricted to small patches and round spots scattered on the back, those in the region of the shoulder of a different color from those of the side and rump patches. Another instance is that of the white-footed mouse of Monomoy Island, Massachusetts, the mid-ventral parts of which are pure white to the roots of the hairs, an albinistic condition to be clearly distinguished from that in which the belly appears white, but only because of the white *tips* to the hairs whose bases are dark-pigmented.

The restriction of the rump patches so as to produce a white tail-tip is common among mammals. It is found in occasional specimens of many species as the shrew mole (*Blarina*), Brewer's mole (*Parascalops*), the meadow jumping mouse (*Zapus*), the white-footed mouse (*Peromyscus*), and squirrels (*Sciurus*). In some it has become developed as a permanent and characteristic mark, as in the woodland jumping mouse (*Napæozapus*), the red fox (*Vulpes*), such genera as *Hydromys, Tylomys,* the Virginia opossum (*Didelphys virginiana*), the tree kangaroos (*Dendrolagus*). In many others a pure white belly is developed through ventral restriction of the shoulder and side patches.

Among ungulates the break between the ear patches has been developed to form a broad white blaze from forehead to nose in case of the blesbok (*Damaliscus albifrons*) of South Africa and in related species in East Africa. The chevron-mark on the forehead of certain antelopes is possibly a specialized development of the same thing.

White buttock patches are present in several unrelated ungulates—as the pronghorn (*Antilocapra*), the wapiti (*Cervus canadensis*), and the Rocky Mountain sheep (*Ovis canadensis*). Probably these are the result of restriction or total inactivity of the pigment patches covering the rump.

FIG. 42*a*. DIAGRAM SHOWING THE PIGMENTED PATCHES OF A PARTIALLY ALBINO DEER.

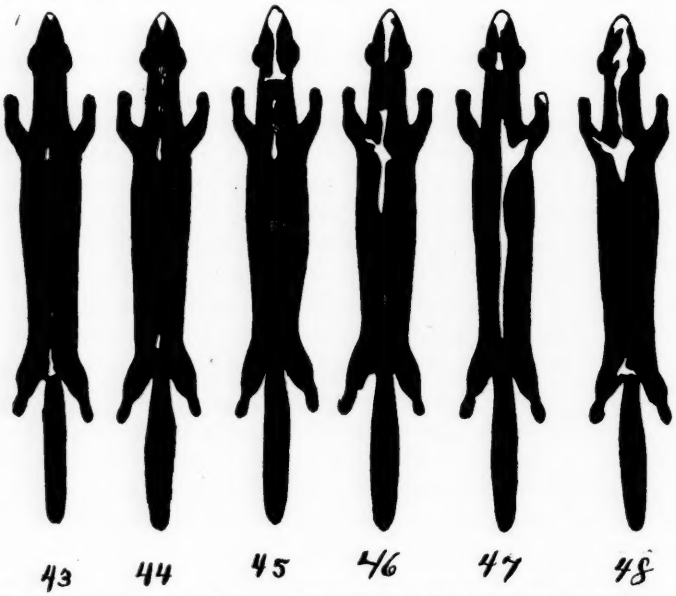
Among the deer family white is generally confined to the under surfaces and the primary white breaks have not been developed to form patterns. Albinistic deer are fairly common, however, and in Fig. 42*a* I have made a tracing from a photograph showing the side of a partially albino doe in which areal restriction of pigment has taken place in such wise that the primary patches are all indicated, and separated from those of the opposite half of the body by a median dorsal white line. The ear and the neck patches are joined, but a few small islands of pigment are left here and there, much as in cows.

In the young of many deer and in the adult of such species as the axis deer, a spotted pattern is developed.

There is an obvious tendency for the spots to become arranged in longitudinal rows, and intermediate stages may be found in which they coalesce to form broken lines. There is little doubt that the complete white stripes occurring in part of this pattern were formed originally through the coalescence of rows of white spots. In the tapir a somewhat similar spotted pattern is found in the young, while the adult Malayan tapir has lost the shoulder and side patches, producing thus a white-bodied animal, pigmented to the back of the foreleg and on the buttocks and hind legs. Among the ground squirrels (*Citellus*) a beautiful series can be picked out showing the transition from a uniform grizzled mixture of ticked hairs to indistinct spotting, then rows of white spots, and finally broken and complete longitudinal stripes. The production of these stripes I believe to be due, not to the development of breaks between the primary pigment patches, but to the action of a factor which is the negative of the so-called "English" marking in rabbits, so that instead of the *development of scattered small pigments spots* there are formed, instead, spots without pigment. That it is possible to evolve a striped pattern from spots through selection, I have no doubt, and indeed, it is generally believed. On the other hand, it is quite possible that the converse may happen, and spots result through the breaking up of stripes. According to the experiments of Professor Castle and Dr. MacCurdy, however, it seems to be a difficult matter to fix a given marking by rigid selection, yet it must be admitted that a few years' work even of careful breeding is nothing in comparison with the age-long selection that may have been at work on the species. That it is a difficult matter to produce a given pattern is further evidenced by the fact that in many species in which white markings regularly occur as part of the pattern, these are subject to great individual variation in their extent, showing that they are even yet not wholly definite.

It was formerly urged against evolutionary doctrine

that we do not now see its processes in action, that species are stable and subject to very little variation. This view, however, was found to rest on faulty observation, for, though some species are fairly stable, others are very plastic and exhibit before our eyes various steps in development. So in case of the development of a particular pied pattern, it is possible to see in certain species the actual course of its formation. Among mammals, the Mustelidæ or weasel family show several instances in



FIGS. 43-48. DIAGRAMS SHOWING RESTRICTION OF PIGMENTATION ON THE VENTRAL SURFACE OF MINKS (*Mustela vison*).

point. The common mink (*Mustela vison*) of northeastern North America is now in process of developing a pure white under side, such as is present in the New York weasel (*M. noveboracensis*) or the smaller Bonaparte's weasel (*M. cicognani*). The diagrams shown in Figs. 43–48 are from the fine series of mink in the collection of the Museum of Comparative Zoology and depicit the

under side of the specimens. In the large coastal race of mink found from southern Maine to the Carolinas (*M. v. lutreocephalus*), the entire pelage is usually brown, except for the chin which is white. Occasional white marks are present in some specimens along the mid-ventral line of the throat and chest, and between the hind legs. In the smaller typical *M. vison* of northern New England northward the white marking is apt to be more extensive, and in no two individuals exactly alike. The diagrams show the ventral markings of a few specimens from New England and Nova Scotia. In Fig. 43 the amount of white is very small. The chin spot, which represents the beginning of a break between the two ear patches at their antero-ventral extremity, is always present and has become now a fixed mark of the species, though variable in extent. A slight break in the center of the chest shows where the two shoulder patches have failed to meet, and a white spot at the anal region indicates a like restriction of the rump patches. Similar spots appear mid-ventrally in Fig. 44, with the addition of a few white hairs, medially at the upper throat, where the ear and neck patches join, and a few more on the lower throat at the line of union of the neck patches of opposite sides. In Figs. 45 and 46 no break is present on the abdomen, but in the former figure, a large transverse break has appeared on the upper throat where the ear patches fail to unite with the neck patches and with each other, and a median line runs forward to join the white of the chin, showing the greater restriction of the ear patches ventrally. An imperfect separation of these patches along the center of the throat has taken place in Fig. 47, and a more considerable break occurs in the same place in Fig. 46. In the Pacific Coast mink (*Mustela vison energumenos*) a well-developed white patch on the chest is rather characteristic, somewhat larger than in Fig. 45. This is due to the ventral restriction of the shoulder patches which fail to meet below. In Fig. 46 this white area is seen with a tongue extending upon the center of the lower throat, and on to

one fore leg, as well as in the mid line of the thorax, marking nearly the anteroposterior limits of the shoulder patch. The neck patches are not separated in this figure but have become so in Fig. 48, so that a continuous line of white runs from chin to chest. In Fig. 47 the shoulder and the side patches have both failed to join ventrally, and thus a broad white line is formed down the center of the belly from the conjoined neck patches to the rump patches. If all these breaks were to be present in a single animal, there would be a narrowed white area along the entire ventral side of the body from chin to anus, extending on to the lower side of the fore legs. Practically this condition exists in another species of the same genus, Streator's weasel (*Mustela streatori*) of the Pacific Coast, in which the throat, chest and belly are white but the width and boundaries of the white area are very variable in different individuals. It is therefore in a stage beyond that which the minks have reached, yet it has not attained the stage in which the white area is of definite and rather constant bounds, as in certain other weasels, for example *Mustela noveboracensis,* in which the white, of the belly extends nearly or quite to the lateral border of the body, but in different individuals varies slightly, and *M. cicognanii,* in which the white area of the belly constantly extends to the lateral boundary of the venter from throat to anus. This is the condition toward which the mink is tending.

Another interesting case in which a pattern mark appears to be evolving through the fixation of a primary break between pigment patches is that of the so-called tayra of South America (*Tayra barbara*) a large Mustelid. The Central American race (*biologiæ*) of this animal is wholly black, but the typical subspecies of Brazil and northern South America is subject to a varying amount of reduction in pigmentation. Curiously, this takes place at the posterior end of the neck patches or at the anterior part of the shoulder patches. Three of five specimens in the Museum of Comparative Zoology are marked in this

way. All have a triangular patch of white at the base of the throat ventrally, as a break between neck and shoulder patches and a partial separation of the neck patches from each other. Each has a *dorsal* mark of white; in the first a narrow linear break between the shoulders; in the second a broader transverse mark, and in the third a square patch of white occupying nearly the width of body between the shoulders to the base of the neck. The white throat marking increases in extent from first to third, just as does the dorsal marking. Probably in time this white mark, now of irregular size and appearance individually, will become a permanent part of the pattern. In this animal the entire head and neck are a grizzled gray as far back as the posterior limit of the neck patches, and the rest of the body is black. This, then, shows that the pigment patches of head and neck are differentiated in color as well, from the patches of the rest of the body. The occurrence of white markings in the back is relatively uncommon in mammals, though white on the under surfaces is common, and, as shown by Mr. Abbott H. Thayer, may be of real service to the animal as a factor in concealment.

In the development of white pattern-marks, the evidence seems to show that these come in at first as small and fluctuating spots, which may be of little effect in the economy of the animal. Their further development might lead to the extinction of the species if they render it too conspicuous to enemies, unless the species at the same time makes use of them or accommodates itself to their revealing effect. Often, no doubt, they may not be a source of danger at all. A case in point may be that of *Sciurus finlaysoni,* a Malayan squirrel, most of the individuals of which are largely marked with white, and of which specimens may be found side by side, varying from an almost entirely pigmented condition to one of completely white coat and black eyes. White squirrels are occasional in other species, as albinos, but these rarely survive more than a generation in the cases I have known, whereas

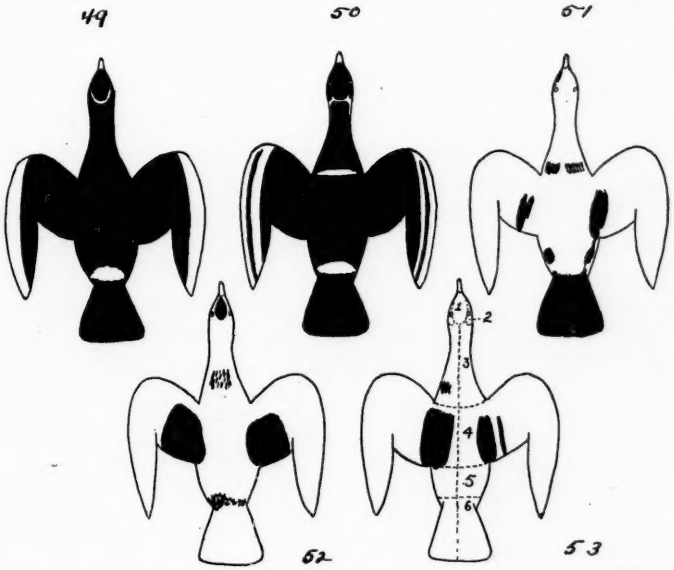
Finlayson's squirrel seems to have accustomed itself by gradual stages to the white condition, so that it is probably not at a great disadvantage by reason of its whiteness.

PIGMENT PATCHES IN BIRDS

In birds the same primary pigment patches seem to be present as in mammals, and they are homologous in the two groups. In defining the extent of the pigment patches, however, allowance must be made for the fact that the long feathers may cover a part of the body remote from their origin. The distribution of the feathers or the pterylosis of the species in hand must also be remembered. In order to arrive at the true interpretation of the patches, it is necessary to consider the pigment as projected back from the vanes of the feathers to the part of the body at their bases. By so doing, it becomes evident that a feather variegated with pigmented and unpigmented (or white) areas indicates none the less that the feather arises from a place of pigment formation. It is only a wholly white feather or patch of feathers that can be considered albinistic in the sense here intended. The factor determining the intermittent formation of pigment in the individual feather is probably a wholly different one from that determining the presence or absence of pigment formation at certain places on the body, though not necessarily different except in its intermittent action.

In the domestic pigeon of our streets and buildings, we have a species that in its wild state is normally fully pigmented except for a white rump patch. Under semi-domestication it has developed partial albinism to a large degree, so that it is possible to obtain a complete series representing on the one extreme a totally pigmented bird without a trace even of the white rump patch, and on the other extreme a bird of pure white plumage. A few of the intermediate stages in areal reduction of pigmentation are shown in Figs. 49 to 53, selected from birds raised for the market and, so far as known, not

bred for pattern. The first steps in reduction are shown in Fig. 49. Here there is seen first a crescentic band of white feathers passing from eye to eye around the occiput. This is a primary break marking off the crown patch posteriorly. This patch in birds, in contrast to its development in mammals, is the main patch of the head,



FIGS. 49–53. DIAGRAMS SHOWING PIGMENTATION IN THE DOMESTIC PIGEON.

covering the area from the base of the bill to the eyes and occiput. In Fig. 50 its posterior limit is similarly defined by a primary break separating it from the neck patches, and although it does not extend forward quite to the eye in this specimen, it shows a beginning of separation from the more lateral ear patches by virtue of the indentations on each side posteriorly. In Fig. 52, the crown patch is shown slightly reduced in extent and wholly separate from the ear patches, which have become inactive altogether. In Fig. 53 it has dropped out with the latter. It is evident then that by greater or lesser

reduction of the crown patch alone it is possible to produce a pigeon with a mere white spot at the back of the head, one with a white stripe from the base of the beak through the eyes to the back of the head (or some part of such a stripe) to a pigeon in which by the total reduction of the patch, the entire top of the head is white. Such specimens can be found in most any miscellaneous flock. There is a tendency often for the patch to be irregularly broken, sometimes divided almost into two parts, a result of the pterylosis to some extent.

The ear patches in pigeons, and probably in all birds, are rather insignificant, and the smallest of all the primary pigment areas. They include the feathers from the posterior angle of the lower mandible to the angle of mouth and thence back, including the ear coverts. I do not feel sure that the patches of opposite sides may not join on the chin, but the present evidence tends to show that the chin is pigmented by a forward extension of the neck patch, which, under reduction, often leaves a small island of pigment between the mandibular rami. In Fig. 50 the neck patches are seen to have broken away anteriorly from the crown and ear patches and the separation of the latter from the crown is indicated by deep reentrants along the line of the separation. In Fig. 51 a remnant of the ear patch of the left side alone remains in dorsal view, consisting of a small tuft of pigmented feathers at the fore end of the aural area and a single pigmented feather just behind it. In this specimen there are a few pigmented feathers on the chin as well, which I take to be an isolated bit of the neck patches.

The neck patches are bilateral in origin, and pigment the entire throat and neck back to a point corresponding to the base of the neck vertebræ. They meet the crown patch and separate the ear patches at the occiput. In the domestic pigeon the neck patches correspond very closely to the area of differentiated feathers that give the metallic reflections. In the reduction of this area it is common for the anterior part of the throat to be white, and then a

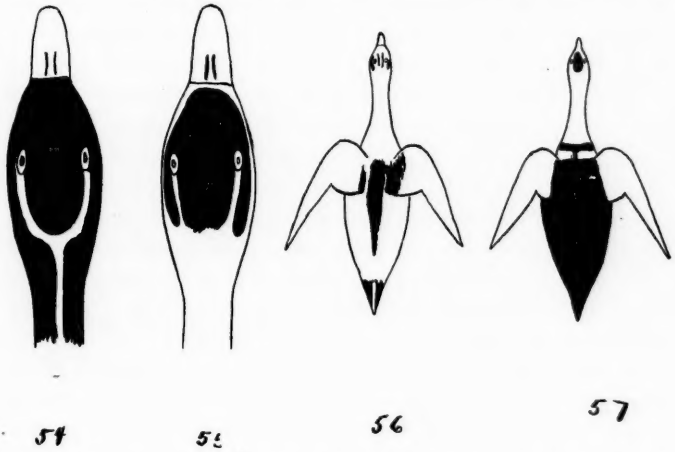
break occurs between the neck patches and those of the head as in Fig. 50. Posteriorly the neck patch under reduction may become separated by a white ring at the base of the neck, from the shoulder patches as in Fig. 50. The ultimate centers of these patches seem to be in the pigeon well back on the base of the neck. These are shown, of small extent, in Fig. 51, as two small areas of pigmented feathers, one on each side of the base of the neck. In Fig. 53, further reduction has taken place, so that the patch of the left side only remains as a small center. In Fig. 52 there is a large median dorsal patch, which, as in mammals, may represent the two centers of opposite sides which even under much reduction have not in this individual become divided medially.

A very common manifestation of pigment reduction in pigeons is to have the primaries or some of them white, as in Figs. 49 or 50. This indicates a failure of pigment to develop at the extremities of the shoulder patches, just as in mammals white forefeet mark a slight reduction of the same areas. It is a fact of much interest that in the guinea fowl (*Numida*), which has been under domestication but a short time comparatively, a distinct breed has arisen in which this same reduction of pigment is present, resulting in a speckled bird with pure white primaries and often a pure white area on the breast. In the pigeon, further reduction cuts off a narrow ring of pigment encircling the breast, or, it may be, broken in the mid-ventral line. This ring represents the reduced shoulder patches, and is to be seen in many wild species as a permanent part of the pattern. The white collar at the base of the neck in Fig. 50 marks the separation between the neck and the shoulder patches at the anterior border of the latter. In other specimens the patches are separated medially by a white area down the back. The ultimate centers of these patches seem to be near the elbow or on the upper arm at the base of the tertiaries, as seen in Figs. 52 and 53.

The side patches are rather small and seem to center, as in Fig. 51, near the groin on either side. They pigment the belly back of the breast area included by the shoulder patches, and extend on to the hind legs as well. In a specimen before me, the shoulder patches pigment the bases of the wings and the entire breast corresponding roughly to the length of the sternum, and tend to be separated by encroaching white feathers midventrally. The side patches are much more reduced, and are confined to a small area at the top of each thigh. The remainder of the patches has become inactive, so that a completely white belly and back result. A very common occurrence is the white rump patch due to the restriction of the side patches, so that a break occurs between them and the tail patches. The rump patches in birds are situated far back, as in mammals, and pigment the tail coverts and the rectrices as in Figs. 49–51. The bilaterality of the two patches is often indicated in pigeons by the occurrence of a few pure white rectrices in the center of the tail. Other birds show pure white feathers at either side of the tail, with a tendency to bilateral symmetry, a most important fact, since it indicates restriction at the outer extremes of these centers. In the restriction of pigment formation, the rectrices are the first to become white, as one would expect, since they are situated at the extremity of the body and farthest from the center of the patch. In Fig. 52 these centers are seen to be at the base of the tail above, and include the upper tail coverts. They are still joined medially, but that of the left side is more extensive than the patch on the right side. The approximate boundaries of the several pigment patches are indicated in Fig. 53 by dotted lines; 1 is the crown patch, 2 the ear patch, 3 the neck patch, 4 the shoulder patch, 5 the side, and 6 the rump patch, as they appear in a dorsal view. Ventrally the neck patch runs forward to the symphysis of the mandibles.

In a flock of domesticated mallard ducks which I studied, the same patches were found indicated, and

some of the details of these are shown in Figs. 54–56. In the male wild mallard there is no white in the pattern of the head and neck except a white ring at the base of the neck. In one of the domesticated breed, shown in Fig. 54, the crown patch was very beautifully marked off, as in the pigeon (Fig. 49), by a white band from eye to eye passing about the occiput. This duck was further interesting in showing the median division of the two neck patches, as a narrow white line running down the



FIGS. 54–57. DIAGRAMS SHOWING PIGMENTATION IN DOMESTICATED MALLARD DUCKS AND IN THE (WILD) LABRADOR DUCK (57).

back of the neck medially, from the occipital stripe. Another duck shown in Fig. 55 had lost the neck patches entirely, but showed the same occipital stripe bounding the crown patch posteriorly, and the ear patches dorsally. The ear patches still adjoin the crown patch anteriorly. In Fig. 56 is represented another of these ducks in which both ear patches are distinct and separate on either side of the head. The crown patch appears as two narrow lines of pigmented feathers which are not quite in contact posteriorly. I have not obtained a satisfactory explanation for the apparent tendency of this patch to

divide medially. Probably for some reason the formation of the pigment is more intense at the sides of the crown than in the center where the nerve and blood supply is less. In the pterylosis of this area the development of feathers is seen to be greater at the sides also.

The neck patches and the side patches are absent entirely, but the shoulder patches are both present, in Fig. 56, that of the right side covering the scapulars and middle of the upper back, that of the left side including a few only of the scapulars.

The tail patches are both present, and separate from each other, as shown by the median white rectrices.

In this same flock of mallards was a female which had a white ring at the base of the neck in the same situation as the white ring which in the male is a part of the permanent pattern. It was not quite complete dorsally, however, in this female, and was somewhat broader than regularly in the male. Nevertheless, it is apparent that this white collar in the male is merely a primary break between neck and shoulder patches that has become developed as a part of the normal pattern.

Stone (1912, p. 318) in his paper on the phylogenetic value of color characters in birds, hints at the existence of these patches. He says, in part:

> In matters of pattern there seems to be a deeper problem involved, *i. e.*, the determination of the cause governing the appearance of a differently colored patch on corresponding parts of the plumage of birds belonging to wholly different groups . . . or the presence of a mystacial stripe, a supereiliary stripe, a light rump patch. . . . In fact if a bird exhibits a bright or contrasting patch of color, it is, in the vast majority of cases, found on one of several definite portions of the plumage, as the crown, the throat, the bend of the wing, the rump, etc.

These contrasting areas are due to the development of one or more of the primary patches, or of breaks between them, or again paler areas, as at the bend of the wing or on the rump, indicate often a lessening of pigment intensity at a distance from the respective primary centers.

(*To be concluded.*)

NOTES ON THE MEADOW JUMPING MOUSE (ZAPUS HUDSONIUS) ESPECIALLY REGARDING HIBERNATION

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THE jumping mouse is the only one of the wild mice of this region (Massachusetts) which exhibits the habit of regular hibernation. Regarding this habit there are a number of references in the literature on the subject. Barton[1] was one of the first to refer to the fact that this mouse became dormant in winter. He says, in describing the actions of one he had in captivity:

> On or about the 22d of November it passed into the torpid state. It is curious to observe that at the time it became torpid the weather was unusually mild for the season of the year, and moreover the animal was kept in a warm room, in which there was a large fire the greater part of the day and night . . . It was frequently most active while the weather was extremely cold in December.

This was in Philadelphia, Pa.

Audubon and Bachman[2] regret that they live in a region where the species does not exist and can not speak from personal observation on the subject.

Godman,[3] Thompson[4] and Kennicott[5] speak of its habit of hibernation.

Tenney[6] gives an account of a specimen of this species taken alive on January 18, 1872, near Vincennes, Ind. It was dormant, coiled up tightly, "the nose being placed upon the belly, and the long tail coiled around the ball-like

[1] "Some Account of an American Species of Dipus or Jerboa," by Benjamin Smith Barton, M.D., *Translations of the Am. Philosophical Society*, Vol. IV, No. XII, 1799.

[2] Viviparous Quadrupeds of No. America," Vol. II, 1851, p. 255.

[3] Godman, "Am. Nat. Hist.," Vol. I, 1842.

[4] Rev. Zadoc Thompson, "Nat. and Civil Hist. of Vermont," 1842.

[5] Kennicott, Patent Office Report for 1857.

[6] Tenney, "Hibernation of the Jumping Mouse," AM. NATURALIST, June, 1872, Vol. VI, No. 6, pp. 330–332.

form which the animal had assumed." It was taken from a nest about two feet below the surface, made of bits of grass. The mouse showed no signs of life at first, but on being held in his hand, soon became feebly active, and on being placed in a warm room, came out of its dormant condition entirely. It again became dormant that night, but was aroused twice again by the application of heat, within the next few weeks, in spite of very cold weather.

Merriam[7] tells of taking an active male at Easthampton, Mass., on February 11, 1872, and states that during the mild winter of 1881–82, in Lewis County, Northern New York, he saw jumping mice active several times.

Seton[8] speaks of finding a *Zapus Hudsonius* on September 27, 1888, at Carberry, Manitoba, in a nest of leaves under the roots of a stump, nearly torpid. He says:

> In the country near Carberry, I never saw it active after September first.

Stone and Cram[9] believe that this mouse passes six months or more of every year hibernating underground. They speak of seeing a family of them turned up by a plough in May and exhibiting not the slightest symptom of life, on being handled or breathed upon.

Burroughs[10] tells of a female jumping mouse in captivity that began hibernating early in November and continued until May, with several intervals of activity, especially after warm weather came on.

Preble[11] says:

> Hibernation varies with the locality, but usually begins about the time of the first heavy frosts and lasts until Spring. The fall pelage is usually assumed and the animals become exceedingly fat before entering winter quarters. Although they often lay up stores of food in nests or burrows during summer, it is not known that they use this food during winter. The animals are generally found singly (sometimes in pairs) in nests at a depth varying from a few inches to two or three feet below the surface. Hibernation sometimes takes place above ground.

[7] C. H. Merrian, M.D., "Mammals of the Adirondack Region," 1884.

[8] E. T. Seton, "Life-histories of Northern Animals," Vol. I.

[9] Stone and Cram, "American Animals," p. 103–104.

[10] John Burroughs, "Squirrels and Other Fur Bearers," pp. 121–124.

[11] E. A. Preble, "Revision of the Jumping Mice of the Genus *Zapus*," U. S. Dept. Agr. N. A. Fauna Series, No. 15, 1899.

On June 25, 1912, a female *Zapus Hudsonius* was taken alive, by the writer, on the edge of a small pond in eastern Massachusetts. It was placed in a small wire cage, and after a few frenzied efforts to escape, became quite tame.

On July 5 it gave birth to five young, blind and hairless; but when the family was transferred to a larger cage, the mouse deserted the young and they soon died. One disappeared mysteriously, and may have been eaten by the mother. The young measured at birth: total length 33 mm.; tail 9 mm.; hind foot 4 mm.

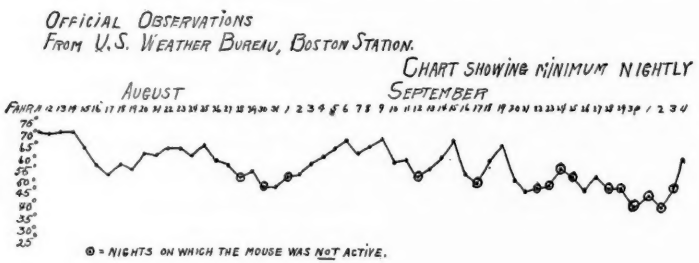
Throughout the summer the mouse ate chiefly rolled oats and shredded wheat, and was also very fond of strawberries and blueberries. It refused most of the common fruits and vegetables.

It was almost wholly nocturnal in its activity, although when disturbed during the day it would immediately begin to eat and remain active for half an hour or more. Toward the latter part of the summer, it seemed to grow quite fat. Rhoads[12] says in this connection:

> When going into winter quarters they are exceedingly fat, as I can testify from experience in removing this tenacious yellow blanket from the skins of them. This fat is their fuel. By spring it is nearly gone.

During the latter part of August there were several very cool nights (49° F. minimum) and on the night of August 28 it did not come out. This fact was apparent from the clean drinking dish, which was placed in such a position that the mouse could not approach without scattering saw-dust in it. The absence was repeated on August 30, and September 1. Throughout September its actions were irregular. Every night until the 21st, with the exception of the 12th and 17th, it was active, but on the 22d disappeared for four nights. It was then active for two more nights (26 and 27) and following that, inactive for six (September 28 to October 3). From October 4 to 28 it was out every night, although not as vigorous as formerly, neither did it eat as much. When approached it seemed to pay no heed, as if in a sort of stupor.

[12] S. N. Rhoads, "The Mammals of Pennsylvania and New Jersey."



There was no evidence of any attempt at storing away a supply of food, although there was ample opportunity. This habit of storing food is mentioned by Hornaday[13] who says:

> In the autumn it stores in the ground quantities of food for winter use, but despite this fact, under certain conditions, it becomes so thoroughly dormant in winter that it seems to be quite lifeless.

According to Seton,[8]

> It is quite ready to respond at any time to any spell of unusually fine, unseasonable weather, even in the depths of winter, and it is probably for these arousing times, as much as for the spring time famine, that it lays up its abundant stores of food.

Preble[11] also mentions this habit, but Shufeldt[14] denies it. He says, in speaking of the deer mouse (*Peromyscus Leucopus*):

> Is it to meet the requirements of his condition that this mouse lays up a goodly stock of food during the autumn? Something the *Zapus* does not do.

Following the period of activity through October, the mouse was inactive on the four nights of October 28, 29, 30 and 31, and reappeared for the last time on the night of November 1, after which it retired for the winter. The cage was placed by an open window of an empty box stall in a stable where the temperature was practically that of out doors. The mouse built its nest in the side of a large sod placed in one corner of the cage.

In spite of a very mild winter, the lowest official tem-

[13] Hornaday, "The American Natural History."

[14] R. W. Shufeldt, M.D., "Chapters on the Natural History of the United States."

perature for this section being only 3° F. (February 10, 1913,) the mouse did not survive the cold weather, and was found dead, when the cage was opened on June 17, 1913.

The nest was found to be located in the extreme end of the sod, only 1½ inches from the top and about 1 inch from the edge. It was roughly oval in shape, being hollowed out of the loam and lined with a few blades of grass. It measured roughly 1¾ inches by 1½ inches and was just large enough to contain the mouse when curled up into a ball. The opening was on the side. Death was probably caused from exposure to continued cold owing to the unprotected location of the nest.

The poor judgment shown in not building the nest securely in the middle of the large sod, and other similar instances of poor management, have led the writer to believe that the intelligence (if that term may be used) of the *Zapus Hudsonius* is of comparatively low grade, much lower, for instance, than that of the deer mouse (*Peromyscus Leucopus*).

The accompanying chart, which is a record of minimal nightly temperatures, according to the official observations of the U. S. Weather Bureau for this section (Boston), shows the activity of the mouse in relation to the temperature during August, September, October and November, and brings out some rather interesting facts. For example, on October 15, 16 and 17, with the minimum nightly temperature 42°, 36° and 42°, respectively, the mouse was active, while on September 22, 23, 24 and 25,

with the minimum nightly temperature of 48°, 49°, 56° and 53° F., respectively, a much warmer series of nights, it remained inactive, And again, after November 1, during a warm spell in which the minimum nightly temperature for November 7 was 64° F., the mouse did not appear.

A study of this chart suggests the question as to how much the temperature has to do with this habit of hibernation.

It is a somewhat general belief that temperature regulates the degree of torpidity.

Barton[1] maintains that

> the torpid state of animals is altogether an accidental circumstance and by no means constitutes a specific character. The same species becomes torpid in one country and not in another. Nay, different individuals of the same species become torpid or continue awake in the same neighborhood or even on the same farm.

Seton[8] believes that

> while torpor is more or less controlled by temperature, the habit of torpidity, like the changing pelage of the white-hare, is so deeply ingrained constitutionally that there is a strong tendency to torpify at a given time without regard to the original cause.

It is evident from this chart that torpidity develops gradually, at first for only one night at a time. Whether this process is explained by a cerebral anemia, a slow toxemia of the brain centers or some other of the theories regarding sleep, it seems to require about two months in which to become sufficiently developed to control completely voluntary body functions. During that interval the animal occasionally awakens, probably from hunger and habit as much as from any effect in change of temperature.

After torpidity is thoroughly established, changes of temperature may be important external factors, as has been demonstrated on numerous occasions in producing a temporary activity by the application of heat. It is safe to say, however, that the temperature is not the only element which influences the length of the period of hibernation.

SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING—IV

On a General Formula for the Constitution of the *n*th Generation of a Mendelian Population in which all Matings are of Brother × Sister[1]

I. In a former paper in this series[2] the constitution of a Mendelian population in which all mating was of the brother × sister type was worked out empirically. The results there presented may be put in the form of a general formula, by means of which the constitution of any generation may be written down from a knowledge of the preceding generation; that is from a knowledge of the $n-1$th generation the nth generation may be at once written down.

II. This general formula may be developed as follows. A single character pair will be considered, A denoting the dominant character and a the recessive. Equal fertility for all matings is assumed, the number of individuals per family being taken as $2s$, of which s are males and s are females. One family will then make s matings and produce s families in the next generation. Each mating is, by hypothesis, of a brother with his sister.

Starting as before with a pair from a population in which all individuals are of constitution Aa there will be in the next generation one family of the $AA + Aa + aA + aa$ type. In all succeeding generations there will be six types of families, viz.:

(1) AA families.
(2) $AA + Aa$ families.
(3) Aa families.
(4) $Aa + 2Aa + aa$ families.
(5) $Aa + aa$ families.
(6) aa families.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 66.

It seems desirable to publish as a general series of "Studies on Inbreeding" the results of certain investigations now in progress in this laboratory. The three papers which have already appeared in this series, without the general title, are: I. "A Contribution towards an Analysis of the Problem of Inbreeding," Amer. Nat., Vol. XLVII, pp. 577–615, 1913. II. "Tables for Calculating Coefficients of Inbreeding," Ann. Rept. Me. Agr. Expt. Sta. for 1913, pp. 191–202. III. "On the Results of Inbreeding a Mendelian Population: A Correction and Extension of Previous Conclusions," Amer. Nat., Vol. XLVIII, pp. 57–62, 1914.

[2] Amer. Nat., Vol. XVLIII, pp. 57–62, 1914.

The proportionate number of each of these types of families will change in successive generations according to the following system.

Let o_{n-1} denote the number of AA families in the $n-1$th generation, and

p_{n-1} denote the number of $AA + Aa$ families in the $n-1$th generation, and

q_{n-1} denote the number of Aa families in the $n-1$th generation, and

r_{n-1} denote the number of AA and $2Aa$ and aa families in the $n-1$th generation, and

u_{n-1} denote the number of $Aa + aa$ families, and

v_{n-1} denote the number of aa families.

It will be possible to write down u and v in any case without calculation because of the symmetrical relations of a Mendelian population, since always under normal conditions such as are assumed in the general treatment, we have

$$\begin{aligned} u_{n-1} &= p_{n-1}, \\ v_{n-1} &= o_{n-1}, \\ u_n &= p_n, \\ v_n &= o_n. \end{aligned}$$

It is necessary, therefore, to consider only the coefficients for the first four types of family. In the nth generation the constitution of the population in respect of *families* (not individuals) will be as follows:

Families in nth generation

$$\begin{aligned} = {} & s(o_{n-1} + 1/4p_{n-1} + 1/16r_{n-1})AA \text{ families} \\ & + s(1/2p_{n-1} + 1/4r_{n-1})AA + Aa \text{ families} \\ & + s(1/8r_{n-1})Aa \text{ families} \\ & + s(1/2p_{n-1} + q_{n-1} + 1/4r_{n-1})AA \\ & \quad + 2Aa + aa \text{ families} \\ & + s(u_n)Aa + aa \text{ families} \\ & + s(v_n)aa \text{ families.} \end{aligned}$$

Or, taking coefficients alone we have

$$\begin{aligned} o_n &= o_{n-1} + 1/4p_{n-1} + 1/16r_{n-1}, \\ p_n &= 1/2p_{n-1} + 1/4r_{n-1}, \\ q_n &= 1/8r_{n-1}, \\ r_n &= 1/2p_{n-1} + q_{n-1} + 1/4r_{n-1}, \\ u_n &= 1/2u_{n-1} + 1/4r_{n-1} = p_n, \\ v_n &= v_{n-1} + 1/4u_{n-1} + 1/16r_{n-1} = o_n. \end{aligned} \qquad \text{(i)}$$

III. Let us see how this formula works out in a concrete case. Assume the same conditions of fertility as in the former paper, that is, put $2s=32$, or $s=16$. Start with a single $AA+2Aa+aa$ family.

Then
$$o_{n-1}=0,$$
$$p_{n-1}=0,$$
$$q_{n-1}=0,$$
$$r_{n-1}=1.$$

Then in the next generation we shall have

$16\{0+1/4(0)+1/16(1)\}=1$AA family
$+16\{1/2(0)+1/4(1)\}=4(AA+Aa)$ families
$+16\{1/8(1)\}=2Aa$ families
$+16\{1/2(0)+0+1/4(1)\}=4(AA+2Aa+aa)$ families
$+4(Aa+aa)$ families
$+1aa$ family.

This is the fact.

In the next generation we shall have

$16\{1+1+1/16(4)\}=36AA$ families
$+16\{1/2(4)+1/4(4)\}=48(AA+Aa)$ families
$+16\{1/8(4)\}=8Aa$ families
$+16\{1/2(4)+2+1/4(4)\}=80(AA+2Aa+aa)$ families
$+48(Aa+aa)$ families
$+36(aa)$ families.

This is the fact.

In the next generation we shall have

$16\{36+1/4(48)+1/16(80)\}=16\times 53=848AA$ families
$+16\{1/2(48)+1/4(80)\}=16\times 44=704(AA+Aa)$ families
$+16\{1/8(80)\}=160Aa$ families
$+16\{1/2(48)+8+1/4(80)\}=16\times 52=832(AA+2Aa+aa)$ families
$+704(Aa+aa)$ families
$+848aa$ families.

Succeeding generations follow the same law and need not be worked out in detail.

IV. So far the discussion has confined itself to families, as this must be the basic unit in the theory of any form of inbreeding. Turning to individuals we have the following simple relations to pass to individuals.

In the nth generation the number of

AA (or aa) individuals $= 2s(o_n) + s(p_n) + 1/2s(r_n)$,
Aa (or aA) individuals $= 2s(q_n) + s(1/2p_n) + 1/2s(r_n)$.

The first of the above expressions multiplied by 2 gives the total homozygotes, and the second multiplied by 2 gives the total heterozygotes.

RAYMOND PEARL

PARALLEL MUTATIONS IN ŒNOTHERA BIENNIS L.

IN the summer of 1912 I cultivated pure strains of *O. biennis* L. and of the *O. biennis cruciata* de Vr. of our Dutch dunes, as well as of their hybrids, made with the purpose of studying the behavior of the *cruciata*-character in crosses. In one of these cultures I unexpectedly obtained two mutants, which because of their similarity to corresponding variants derived from *O. Lamarckiana* have been called *O. biennis nanella* and *O. biennis semi-gigas.* The first mutant, *O. biennis nanella,* occurred in the second generation of the cross *O. biennis* × *O. biennis cruciata* and differed from *O. biennis* in all those points which separate *O. Lamarckiana nanella* from *O. Lamarckiana.* The other variant, *O. biennis semi-gigas,* appeared in the second generation of the reciprocal cross, *O. biennis cruciata* × *O. biennis,* suggesting immediately by its much more vigorous habit and especially by the larger size of its buds and flowers the differences between *O. Lamarckiana* and *O. gigas.* A count of its diploid number of chromosomes proved it to deserve the name *semi-gigas,* 21 chromosomes being shown by nuclear plate-stages in the meristematic tissue of young buds. From these facts, showing that *O. biennis* is in a mutating condition, I drew the conclusion that the phenomenon of mutation in the genus *Œnothera* is older than the species *O. Lamarckiana—O. biennis* generally being considered to be an older species than *O. Lamarckiana*—and further, that the mutations in this group can not be the result of hybridization, as was assumed by some authors at that time—nobody doubting of the purity and constancy of *O. biennis.* As a matter of fact, both of my mutants have been derived from crosses between *O. biennis* and *O. biennis cruciata.* But I laid special emphasis on the fact that *O. biennis* and *O. biennis cruciata* have exactly the same germinal constitution except for the factors that determine the shape of the petals, *O. biennis cruciata* being prob-

ably a mutant from *O. biennis* itself. Therefore, hybrids between these two forms can be looked upon as pure *O. biennis* except for floral characters.

With this conception Bradley Moore Davis does not agree.[1] He thinks that the *O. biennis* and *O. biennis cruciata* of our dunes are not so closely related types, that a cross between them can be treated "as though it were the combination of forms within the same species which have similar germinal constitutions." He says:

> It should be made clear that the form "*O. biennis cruciata*" is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters. . . . *O. cruciata* is found wild in certain regions of New England and New York and is consequently a native American species. . . . Whatever may have been the origin of *O. cruciata* or its possible relationship to *O. biennis*, a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product a hybrid in which marked modifications of germinal constitution are to be expected.

From Davis's point of view I "really made a cross between two rather closely related species" and obtained in the second generation "two marked variants due to some germinal modifications as the result of the cross." In so far as my observations bear upon the problem of mutation Davis's interpretation is exactly the reverse of mine. To him they further illustrate the same phenomenon which he is obtaining through his "hybrids of *biennis* and *grandiflora*, namely, that behavior by which these hybrids in the F_2 generation throw off variants that in taxonomic practise would be considered new species readily distinguished from the parents of the cross and from the F_1 hybrid."

It will be shown in the following lines that the objections made by Davis are not sufficiently justified. My argument consists of two points.

In the first place, Davis is mistaken as to the nature of the *O. biennis cruciata* de Vr. of our dunes. This strain is in reality quite another type than the different forms of the American *O. cruciata* Nutt., called by some authors *O. biennis cruciata*. With this species it has in common only the character of the narrow

[1] Bradley Moore Davis, "Mutation in *Œnothera biennis* L.?" THE AMERICAN NATURALIST, Vol. XLVII, 1913, pp. 116–121; "Genetical Studies on *Œnothera*," IV, THE AMERICAN NATURALIST, Vol. XLVII, 1913, pp. 546–571.

petals, all other features of the stem, foliage, flowerspikes and fruits being exactly those of the Dutch *O. biennis* L. It must certainly be looked upon as a mutation from the *O. biennis* L. of our sand dunes. Until now it has only been found a couple of times in single individuals in the midst of the ordinary *O. biennis,* the first time in 1900 by Dr. Ernst de Vries in the dunes in the neighborhood of Santpoort, Holland, in one individual—and from this one specimen all the subsequent generations of *O. biennis cruciata* in the cultures grown by de Vries and by myself have been derived. Besides this, our *O. biennis* and *O. biennis cruciata* are so similar to one another except for floral structure that plants of both types can not be separated before the flowers open. Therefore we have the right to assume that the crossing of these two forms is concerned alone with the floral characters and that with respect to all other characters parents as well as hybrids are mere *biennis.* Therefore the two variants which arose in my cultures from crosses between *O. biennis* and *O. biennis cruciata* obviously prove the faculty of mutation in *O. biennis.*

In the second place I have found now that it is not necessary to cross *O. biennis* with *O. biennis cruciata* in order to obtain the above named mutants, as Davis seems to believe. Already in his new book Professor de Vries figures a dwarf derived from *O. biennis cruciata* grown in pure line. Shortly afterwards I myself obtained six mutants from the *O. biennis* of our sand dunes grown also in pure line. A few details about these cultures of last year may be given here. In all they counted 920 individuals, 430 of which belonged to the third and 490 to the fourth generation of a pure line, the point of departure for which had been one individual brought into the experimental garden in the rosette stage from the dunes near Wyk aan Zee in the beginning of 1905 and self-fertilized in the same year. The six mutants which appeared in these pure cultures of *O. biennis* were the following. First a dwarf, then a *biennis semi-gigas* having 21 chromosomes and finally four individuals of the *O. biennis sulfurea,* a pale-flowered form of *O. biennis,* which had been found already several times in our dunes in the midst of the ordinary *biennis,* but was not with certainty known to be a mutant from the latter form until now. The two first named mutants and one *sulfurea* appeared in the third generation of our pure line, the *nanella* and the *semi-gigas* coming from the same mother. The three remaining *sulfurea*-individuals appeared in the fourth generation, all

descending from the same motherplant. Of these mutants the *nanella* and *semi-gigas* are especially valuable because similar forms have been produced by *O. Lamarckiana.* It will be seen that the *biennis*-dwarfs seem to be somewhat rarer than the dwarfs of *Lamarckiana.* Whilst for the latter the mutation coefficient is about 1 per cent., our *O. biennis nanella* appeared as the only dwarf among 920 individuals. The above cited *O. biennis cruciata nanella* was the only dwarfed individual in a culture of 500. And the dwarf which I got in 1911 was the only one among about 600 plants. In this connection I wish to recall the conclusion reached by de Vries that in *O. Lamarckiana* the pangen for tall stature must be assumed to be present in the labile condition on both sides, in *O. biennis,* however, only in the male sexual type, whilst in the female sexual type active alta-pangens have to be supposed. The way from *biennis* to *biennis nanella* might therefore possibly be somewhat longer than the one from *Lamarckiana* to *Lamarckiana nanella.* The *biennis semi-gigas* which appeared in the last summer corresponded in all points exactly with the mutant of 1911. Moreover a count of the chromosomes, as shown by nuclear plate-stages in the meristematic tissue of young buds, determined them to be 21 in number. Even as the specimen of this type, that appeared in 1911, and as the *semi-gigas* mutants produced by *O. Lamarckiana,* the plant of last year proved to be almost absolutely sterile.

In his second above-mentioned paper Davis says about the *O. biennis* of our dunes: "No species of *Œnothera* is perhaps so free from suspicion as to its gametic purity. If Stomps can obtain mutations from tested material of the Dutch *biennis* grown in pure lines he will have the basis of a strong argument. . . ." Fortunately the experiment asked for by Davis, has been made in the same year as his criticism. The Dutch *biennis* L., cultivated in pure line, has produced a dwarf, a *semi-gigas* and some *sulfurea*-individuals, proving its mutability beyond all doubt. I therefore trust that the conclusions arrived at in my first paper, concerning this mutability and its consequences, may now be accepted as thoroughly valid.

THEO. J. STOMPS

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IN a recent review[1] of Stomps's studies on *Œnothera biennis* L.[2] from the sand dunes of Holland I protested against his designating as mutants a *nanella* type and a *semi-gigas* type which were obtained in the second generation of crosses between *Œnothera biennis* Linnæus and its variety *O. biennis cruciata* de Vries. The criticism was presented on the general ground that however close the possible relationships between the two parent forms, they nevertheless constituted lines so far apart as to render unsafe a conclusion that marked variants obtained from their crossing are mutants in the sense of de Vries and Stomps. Such variants, it seemed to me, might have been the result of hybridism between two lines sufficiently divergent to upset the similarity of germinal constitution shown in their vegetative morphology, for the species *biennis* and its variety *cruciata* are said to differ only in their flower structure.

In that review I incorrectly associated *O. biennis cruciata* de Vries with *O. cruciata* Nutt., an American species entirely distinct from the variety *cruciata* of de Vries, which has been found only once (in the year 1900) on the sand dunes of Holland among plants of *O. biennis*. I greatly regret my confusion of these two types, since I was led in my criticism to regard Stomps's crosses between *biennis* and *biennis cruciata* as though they were crosses between two distinct although possibly closely related species. In this I was clearly mistaken, since all of the evidence short of experimental proof, which Stomps may yet obtain, indicates that *biennis cruciata* de Vries is a variety of *biennis* L. and arose as a mutation on the sand dunes of Holland. The crosses of Stomps are, therefore, to be regarded as between a species and its mutant variety. I trust that the mutationists will accept this acknowledgment of an error.

There is, I believe, a body of naturalists for whom the value of evidence for mutation rests fundamentally upon the unquestioned purity of the parent stock, and to them any cross, no matter how close, is open to criticism. Stomps has justified his first conclusions by obtaining in later studies the same mutants *biennis nanella* and *biennis semi-gigas* from lines of the pure species *O. biennis* Linnæus. Had he waited for these later results before

[1] Davis, B. M., "Mutations in *Œnothera biennis* L.?" AMERICAN NATURALIST, Vol. XLVII, p. 116, 1913.

[2] Stomps, T. J., "Mutation bei *Œnothera biennis* L.," *Biol. Centralb.*, Vol. XXXII, p. 521, 1912.

publishing on the first there could have been no objections to his main contention that *O. biennis* from the sand dunes of Holland is capable of giving rise to true mutants.

Stomps is continuing his studies on this same Dutch *biennis* with the view of determining its possible powers of mutation; and it is a pleasure to review his second paper[3] which presents some extremely interesting data, a paper in which no important criticism can be based on the source and character of the material employed. No wild species of evening primrose has been so long under experimental and field observation or is better known to the workers with œnotheras than this plant. The species has proved uniform in culture to a remarkable degree and it would be difficult to find a type of *Œnothera* so free from suspicion of gametic purity. The species appears to have been in Holland since pre-Linnæan days and is therefore very old. As material for experimental studies on mutation the Dutch *biennis* seems to the writer the best of all the œnotheras so far brought into the experimental garden.

The starting point of Stomps's cultures of *Œnothera biennis* was a plant transplanted from the sand dunes in 1905. From seed of this plant, self-pollinated, a second generation was grown in 1910, three selfed plants of which gave the seed for a third generation of 430 individuals, and a fourth generation of 490 plants was grown from two selfed plants of the third generation. Thus in all 930 individuals were observed in the third and fourth generations from the plant that gave rise to these pure lines. It is true that these lines have not been under selection for many generations, but, considering the stability of the species and its habit of close pollination, it is very improbable that the source of the cultures should have been a plant not representative of the type. Furthermore, Stomps presumably will continue indefinitely the lines now established and thus determine through later generations whether their mutating habits remain constant.

Among the 430 plants of the third generation there appeared 1 *biennis nanella,* 1 *biennis semi-gigas* and 1 individual of *biennis sulfurea;* the first two came from the same mother plant. Among the 490 plants of the fourth generation appeared 3 individuals of *biennis sulfurea,* all from the same selfed mother. The variety *sulfurea* differs from the species *biennis* in having flowers of a

[3] Stomps, T. J., "Parallele Mutationen bei *Œnothera biennis* L.," *Ber. deut. bot. Gesell.,* Vol. XXXII, p. 179, 1914.

lighter yellow, and is reported by de Vries to be not uncommon in the wild state mixed with the species proper. *Sulfurea* has been held systematically to be a variety of *biennis* but this is the first time that it has appeared in the experimental garden as a derivative of that species. Thus out of a total of 920 plants there were 4 individuals of the color variety *sulfurea,* 1 *nanella* and 1 *semi-gigas,* in all 6 mutants, a showing that may well gratify Stomps.

The mutant *biennis nanella* differed from typical *biennis* in much the same way that *Lamarckiana nanella* differs from *Lamarckiana* and like the latter dwarf showed evidence of a bacterial infection. Certain selfed flowers set no seed because of diseased stigmas. Other flowers pollinated from pure *biennis* set good fruit. The ratio of the appearance of *biennis nanella* is much lower than the mutation coefficient of one per cent. which de Vries has reported for *Lamarckiana nanella.* It should also be remembered that de Vries[4] obtained a *cruciata nanella* in a culture of 500 plants from *O. biennis cruciata.*

The mutant *biennis semi-gigas* in comparison with typical *biennis* showed a stronger habit, broader leaves, thicker buds, larger flowers, supernumerary stigma lobes, and the presence of 4-cornered pollen grains. Counts of the chromosomes in meristematic tissue determined the number to be 21. Therefore in this plant, as in the *biennis semi-gigas* obtained by Stomps from the cross *cruciata* × *biennis,* there is clear cytological evidence that one of the gametes which formed the zygote contained 14 chromosomes, *i. e.,* double the number characteristic of the gametes of *Œnothera.* This is another case of triploid mutants in *Œnothera* to be added to the list of Stomps and Miss Lutz. The plant was self sterile, but set fruit when pollinated by *biennis,* although the yield of seed was very poor.

Stomps is justified in calling attention to the agreement of his second *biennis nanella* with the plant derived in 1911 from the cross *biennis* × *cruciata,* and of the agreement of his second *biennis semi-gigas* with the plant from the cross *cruciata* × *biennis.* It is to be hoped that he will next obtain the *cruciata* variety as a direct mutant from the Dutch *biennis* and thus establish its relationship and origin beyond all possible doubt.

Stomps has before him the opportunity of making through the study of *Œnothera biennis* very important contributions to our

[4] See "Gruppenweise Artbildung," p. 299 and Fig. 108.

knowledge of the frequency of mutations and their importance in organic evolution. That retrogressive mutations take place is not likely to be seriously doubted by any one who has followed the experimental work of recent years both botanical and zoological. The loss of characters through germinal modification, even in what seem to be "pure lines," appears to be not uncommon.

Most of all is desired information on the possibilities, frequency and character of progressive mutations. Can the mutation theory satisfactorily explain progressive advances in organic evolution or must amphimixis chiefly carry that responsibility? Mutants of the tetraploid *gigas*-like type would appear to be progressive, and we can see the reason in their doubled chromosome count which gives larger nuclei, larger cells and modified tissues. *Gigas*-like forms are however very rare and in *O. Lamarckiana gigas* the fertility is relatively low. More common are the triploid *semi-gigas* forms, but these seem to be sterile or almost sterile when selfed, and the work of Geerts indicates that the triploid number in *Œnothera* returns to the normal through the elimination of supernumerary chromosomes. Very interesting is the recent paper of Gates and Thomas[5] which offers evidence that *lata*-like characters are associated with the presence of a single additional chromosome.

And what of the series of forms which differ from the *Œnothera* parent types with as yet no evidence of peculiarities in their chromosome count, *brevistylis, lævifolia, rubrinervis, obovata, scintillans,* etc. Will forms similar to these and perhaps others in addition be represented in a series of derivatives from *Œnothera biennis?* The mutants *biennis nanella* and *biennis sulfurea* belong to this group and have already been obtained by Stomps. One may almost envy him his opportunity for an intensive study of this species.

BRADLEY MOORE DAVIS

UNIVERSITY OF PENNSYLVANIA,
June, 1914.

[5] Gates, R. R., and Thomas, N., "A Cytological Study of *Œnothera* mut. *lata* and *Œ.* mut. *semilata* in Relation to Mutation," *Quart. Jour. Mic. Sci.*, Vol. LIX, p. 523, 1914.

THE THEORETICAL DISTINCTION BETWEEN MULTIPLE ALLELOMORPHS AND CLOSE LINKAGE

PROFESSOR CASTLE'S difficulty in understanding the distinction made by Mr. Dexter[1] is owing to his unfamiliarity at first hand with the phenomenon of linkage. The distinction between allelomorphs and close linkage has already been given several times elsewhere and need not be repeated; but if Professor Castle has failed to note it, or to see its significance, it is probable that others may have done the same. I may be pardoned, therefore, for attempting once more to show why, for clear thinking, it is important to keep in mind the difference between allelomorphs and close linkage. Furthermore, since we have here one of the newest developments of Mendelism, it seems to me that it may be worth while not to let Professor Castle's criticism pass unchallenged.

Dexter pointed out that the mode of treatment that Nabours followed in the analysis of his results is the procedure of multiple allelomorphism, although Nabours does not seem entirely conversant with the fact, but treats the results as though they were regular phenomena. In one case, however, Nabours got an unconformable individual. Dexter points out that if this case is not due to non-disjunction (a known process that will cover such cases) it shows that here at least the factors involved are not allelomorphs, but must be treated as though closely linked.

How could the matter be put more directly? I confess I am at somewhat of a loss to discover why Professor Castle is confused. Perhaps it is the subsequent development of Dexter's explanation that has troubled him. Let us again try to make the distinction clear.

If the factors B and E are not allelomorphic to each other then each must have another allelomorph. This is nothing but pure Mendelism, which no one will, I suppose, dispute. It is entirely irrelevant whether we use small letters or none at all (as Castle prefers) for the allelomorphs. If they are a part of the Mendelian machinery, who cares very much what we call them?

If then we have here two pairs of allelomorphs, crossing over may take place, as it does in other cases where two pairs of linked

[1] THE AMERICAN NATURALIST, June, 1914, p. 383.

genes are involved.[2] This is all there is to the matter. We need not dwell, therefore, at length on Professor Castle's statement that here is another case of an erroneous conclusion reached in consequence of using small letters for "absent" characters, except to remark that Dexter did not use small letters for absent characters, and that the erroneous conclusion has been drawn by Professor Castle himself.

T. H. MORGAN

COLUMBIA UNIVERSITY

PROFESSOR MORGAN has called my attention to the fact that in criticizing a single point in Mr. Dexter's review I have given the impression, to some at least, that I regarded Dexter's views as erroneous. Such was not my intention, and I wish to correct the impression, if I may. I do not for a moment question the reality of "unit-character" inheritance or indorse the idea of "the organism as a whole" as the only inheritance unit. I agree here entirely with the view which I understand Dexter to hold. If Nabours has encountered nothing but simple allelomorphs among his grasshoppers (which I neither assert nor deny), this by no means proves that only simple allelomorphs exist even among said grasshoppers. An organism which seems to have only one variable "gene" may nevertheless possess any number of other genes which are not varying so far as we can discover, and in which consequently all zygotes are homozygous and all gametes similar to each other.

It is only in Dexter's discussion of the significance of the exceptional *"B E I"* individual that I should dissent from any part of his excellent review. Nabours's explanation of this case, according to Dexter, is essentially that of "non-disjunction," instead of which Dexter himself offers the explanation of "linkage," and proposes a repetition of the experiment to decide between them. Now I do not question for a moment the genuineness of either "non-disjunction" or "linkage," as they occur for example in *Drosophila*. Through the kindness of Professor Morgan I have been able to demonstrate both these phenomena repeatedly to classes in genetics in the course of their laboratory work upon *Drosophila*. The point which I wished to make in com-

[2] Crossing over would not take place if the factors in question were allelomorphic. If the case is one of non-disjunction the subsequent generation would also give a different kind of result from that of linkage. (See Bridges, *Jour. Exp. Zool.*, 1913.)

menting on Dexter's review (and this is the *only* point in which I dissent from his opinions) is that the repetition of the experiment, provided it had the outcome suggested by Dexter, would leave us as much in the dark as we were before concerning the correct interpretation of the result. Very likely, however, *additional* facts might be observed which *would* give some clue, so that I quite agree with Dexter's suggestion that the case should receive further study. But I can not see that *at present* linkage has more in its favor as an interpretation than non-disjunction.

The "demonstration" which Mr. Dexter gave of his argument by introducing duplicate "symbols" instead of the single set used by Nabours, seemed to me quite superfluous and possibly to have been a real stumbling block in the logical process. This is why I raised the question as to the significance of the small letters. The terminology is that of the "presence-absence" hypothesis, as commonly understood, but Professor Morgan assures me that such is not the significance which Dexter attaches to the symbols used. It seems to me therefore that the significance attached to the symbols is vital to the argument in the "demonstration."

I quite agree with Professor Morgan, however, that symbols are a matter of small consequence. Suppose we omit the "demonstration" by means of symbols altogether. Should we then have any reason to favor linkage as an interpretation rather than non-disjunction? I can not see that we should have. It seems to me quite possible that neither explanation will prove adequate.

When albino mammals are crossed with colored ones, piebalds sometimes are obtained in later generations. So far as we know, these result neither from "non-disjunction" nor from "crossovers." Perhaps the *B E I* individual also is a *tertium quid*.

W. E. CASTLE

NOTES AND LITERATURE

BIOMETRICS

An Important Contribution to Statistical Theory

One of Pearson's most valuable contributions to statistical theory is his test for goodness of fit.[1] It enables one, with the aid of Elderton's[2] tables, easily to determine the probability that a given system of observed frequencies does or does not differ significantly from a series of theoretical frequencies supposed to graduate the observations. The significance of this criterion in Mendelian work has recently been pointed out by Harris.[3]

Hitherto this criterion has found an important limitation in the fact that, as originally developed by Pearson, it was applicable only to frequency systems. It could be used to test goodness of fit only where the observations were counts of the number of times particular classes of events occurred. But, of course, frequency systems comprise only one kind of observational data to which one has occasion to fit curves. Much more often there is need for a criterion of goodness of fit where the observations are of the nature of true ordinates, rather than frequencies. Such cases include all data of the sort where a mean y is determined for each x, as in a growth curve; or in the regression observed in a correlation table, where for each successive value of one of the variables the mean value of the correlated variable is calculated. There has been no method of testing the goodness of fit for such curves. From a visual inspection of the plotted regression line one has been compelled to form his judgment as to whether it was or was not a good fit.

Recently a Russian statistician, E. Slutsky,[4] has extended

[1] Pearson, K., "On the Criterion that a Given System of Deviation from the Probable in the Case of a Correlated System of Variables is Such that it Can be Reasonably Supposed to Have Arisen from Random Sampling," *Phil. Mag.*, 5th Series, Vol. L, pp. 157–175, 1900.

[2] *Biometrika*, Vol. I, pp. 155–163.

[3] Harris, J. A., "A Simple Test of the Goodness of Fit of Mendelian Ratios," Amer. Nat., Vol. 46, 1912, pp. 741–745, 1912.

[4] Slutsky, E., "On the Criterion of Goodness of Fit of the Regression Lines and on the Best Method of Fitting Them to the Data," *Jour. Roy. Stat. Soc.*, Vol. LXXVII, Part I (December, 1913), issued 1914, pp. 78–84.

Pearson's theory to cover the class of curves, formerly not amenable to such test. The result forms an extremely valuable extension of biometric theory.

Briefly Slutsky's essential result may be put as follows. He finds (the complete proof is not given in this paper) that

$$\chi^2 = S\left(\frac{n_{x_p} e_p^2}{\sigma^2_{n_{x_p}}}\right),$$

where χ^2 is the quantity denoted by the same letter in Pearson's original work, and is the argument in Elderton's table; n_{x_p} is the frequency in the x_p array, *i. e.*, the number of observations on which each observed ordinate is based; e_p is the difference between the observed and the calculated mean y for each x_p array; and $\sigma_{n_{x_p}}$ is the standard deviation of each x_p array; *i. e.*, the standard deviation of the group of observations from which each particular y was calculated. S, as usual, denotes summation. Knowing χ^2, P is read directly from Elderton's tables.

Slutsky gives a couple of examples of the application of the method in his paper. For illustration here I have preferred to take an example from my own unpublished data. The observations (y_{x_p}) in this case are the mean butter productions of American Jersey cattle, based on seven-day tests.[5]

The theoretical points Y_{x_p} are calculated from the equation,

$$y = 14.21098 + .0250x - .0038x^2 + 3.0104 \log x,$$

the constants of which were determined from the observations by the method of least squares.

The test for goodness of fit is carried out in Table I. It should be said that, following the suggestion given by Slutsky in his paper, I have used in the $\sigma_{n_{x_p}}$ column the graduated rather than the observed values. In the present case the scedastic curve is hopelessly far from a straight line. It is, in point of fact, logarithmic.

From this table we have $\chi^2 = 32.115$. This is beyond the range of Elderton's table. By a rough, but sufficiently accurate, graphical extrapolation, I find for present values of n' and χ^2,

$$P = .417 \text{ about.}$$

In other words, if the butter production of Jersey cows changes with age according to the curve given, we should expect to

[5] For data see "Jersey Sires and Their Tested Daughters," published by American Jersey Cattle Club, New York, 1909.

get a worse agreement between observation and theory in 42 out of every 100 random samples on which the point was tested. In other words, the fit may be considered sufficiently good. As a matter of fact, the fit is extraordinarily close over most of the curve. Four (only) out of the 32 ordinates contribute more than 50 per cent. of the value of χ^2.

TABLE I

Age in Years	Observed Butter Production in Lbs.	Calc. Butter Production in Lbs.	Errors	Frequency	Standard Dev. of Arrays	
x_p	y_{x_p}	Y_{x_p}	$e_p = (Y_{x_p} - y_{x_p})$	n_{x_p}	$\sigma_{n_{x_p}}$	$\frac{n_{x_p} e^2_p}{\sigma^2_{n_{x_p}}}$
1.25	14.25	14.23	.02	2	.04	.500
1.75	15.15	15.15	.00	46	.97	.000
2.25	15.57	15.69	.12	273	1.49	1.771
2.75	15.96	16.06	.10	312	1.83	.932
3.25	16.38	16.35	.03	545	2.07	.114
3.75	16.72	16.57	.15	511	2.25	2.271
4.25	16.92	16.74	.18	704	2.38	4.027
4.75	17.09	16.89	.20	532	2.49	3.432
5.25	17.01	17.00	.01	556	2.56	.008
5.75	17.07	17.09	.02	382	2.62	.022
6.25	16.98	17.16	.18	419	2.65	1.933
6.75	17.04	17.21	.17	277	2.68	1.114
7.25	17.09	17.25	.16	285	2.68	1.016
7.75	17.48	17.27	.21	190	2.68	1.167
8.25	17.30	17.28	.02	166	2.67	.009
8.75	17.17	17.27	.10	121	2.64	.174
9.25	17.56	17.25	.31	109	2.61	1.515
9.75	16.67	17.21	.54	95	2.57	4.194
10.25	17.05	17.17	.12	63	2.52	.143
10.75	17.42	17.11	.31	39	2.46	.619
11.25	16.95	17.05	.10	54	2.40	.094
11.75	17.00	16.97	.03	28	2.33	.005
12.25	17.05	16.88	.17	20	2.26	.113
12.75	16.54	16.79	.25	7	2.18	.092
13.25	16.34	16.68	.34	11	2.09	.291
13.75	18.14	16.56	1.58	9	1.99	5.673
14.25	15.89	16.44	.55	7	1.88	.599
14.75	16.15	16.30	.15	5	1.77	.036
15.25	16.37	16.16	.21	4	1.65	.065
15.75	15.75	16.00	.25	2	1.53	.053
16.25	15.42	15.84	.42	3	1.40	.117
16.75	15.75	15.67	.08	4	1.27	.016
Totals ...				5,781		32.115

It may be said, in conclusion, that Slutsky's contribution is one which will be highly valued by all investigators who have a critical interest in the graduation of observational data, whatever the field in which they may be working.

RAYMOND PEARL

A NEW MODE OF SEGREGATION IN GREGORY'S TETRAPLOID PRIMULAS

IN a recent paper[1] Gregory reports a very interesting case in which two different races of *Primulas* suddenly gave rise to giant tetraploid forms, having double the usual number of chromosomes, and apparently having the factors doubled also (individually), for this was true of all the factors which could be followed in his hybridization experiments. It is important to know how segregation will take place in such individuals, as there are four allelomorphs of each gene present.

Let us suppose that a tetraploid form pure for the dominant factor A $\left(\text{and therefore of composition } \frac{A}{A}\frac{A}{A}\right)$ is crossed with a pure recessive giant $\left(\frac{a}{a}\frac{a}{a}\right)$. Gametes AA and aa will meet in fertilization, forming the hybrid $\frac{A}{a}\frac{A}{a}$ (the maternally derived genes are represented on one line, say the upper, the paternally derived genes on the other line).

Now, if this were an ordinary case of "multiple factors"[2] in a diploid organism, although the two dominant factors, which we may again call A's, may produce the same effect upon the organism, yet they are not interchangeable, and the same is true of the recessive factors. That is, if we call both dominants A, we must designate one of them as A^1, and the corresponding recessives must also be designated as a and a^1, for A will always segregate into a different gamete from a, and A^1 from a^1, there being two distinct allelomorphic pairs. On the chromosome view of heredity, we would say that A and a always lay opposed to each other, in homologous chromosomes, on the spindle of the reduction division, as did also A^1 and a^1, but neither A nor a lay in chromosomes homologous to those of either A^1 or a^1, and assorted independently of them. The line-up of factors on the spindle in the reduction division in this case would be equally likely to be $\frac{A}{a}\frac{A^1}{a^1}$ or $\frac{A}{a}\frac{a^1}{A^1}$, depending merely upon which

[1] R. P. Gregory, "On the Genetics of Tetraploid Plants in *Primula sinensis*," *Proceedings of the Royal Society*, 1914.

[2] *i. e.*, a case where two (or more) independent pairs of factors produce similar effects, upon the same character. Many examples of this are known, *e. g.*, the inheritance of red flower in flax.

way the pairs are turned with reference to each other. The first alignment gives gametes AA^1 and aa^1, the second gives Aa^1 and aA^1. Thus three gametes with a dominant factor to one pure recessive would on the average be produced, the ratio being 1AA : 2Aa : 1aa, omitting primes.

In a tetraploid form, however, A and A^1 are alike and interchangeable, as also are a and a^1. In the hybrid $\frac{A}{a}\frac{A^1}{a^1}$, therefore, there would be at least one other mode of pairing of allelomorphs possible, giving two new modes of line-up on the reduction spindle, and they would occur just as frequently as the two previous kinds. The two new arrangements would be $\frac{A}{a^1}\frac{A^1}{a}$, giving gametes AA^1 and a^1a, like those in the first of the two previous cases, and $\frac{A}{a^1}\frac{a}{A^1}$, giving gametes Aa and a^1A^1.[3] These latter gametes would be indistinguishable from the Aa^1 and aA^1 gametes given by the second of the two usual arrangements unless A could be distinguished from A^1 and a from a^1. This could happen only if the allelomorphs were of four different kinds or if there were linkage of these genes with other genes for which the plant was heterozygous. Unless, therefore, linkage or multiple allelomorphism were involved, we could not distinguish between this mode of pairing of allelomorphs and the usual kind; both would give three gametes containing at least one dominant, to one pure recessive (*i. e.*, 1AA : 2Aa : 1aa, omitting primes).

Still a third type of pairing of allelomorphs is possible in a tetraploid plant, however. There seems no *a priori* reason, on the chromosome view, why, in a tetraploid plant, a gene should have to segregate from one of the allelomorphs derived from the opposite parent. That is, in a plant of composition $\frac{A}{a}\frac{A^1}{a^1}$, paternally derived genes being indicated on, say, the upper line, maternally derived ones on the lower, there is no apparent reason why the line-up of chromosomes at reduction should not be $\frac{A}{A^1}\frac{a}{a^1}$ $\frac{A}{A^1}\frac{a^1}{a}$ or as often as it is one of the other types, since all four chromosomes are homologous. Thus we should get gametes Aa, A^1a^1, Aa^1 and A^1a.

[3] If linkage with other genes could be followed, we should with this mode of pairing obtain crossing over between the chromosomes containing A and a^1, respectively, and between those containing A^1 and a, respectively; this would not occur on any other mode of pairing.

We could distinguish such gametes individually from those obtained by the ordinary arrangements only if linkage were involved, for then we should sometimes obtain results indicating that the chromosomes containing A and A^1 had crossed over with one another, and so had probably behaved as homologous chromosomes at the reduction division. However, we could also determine whether this mode of pairing occurred or not merely by determining the relative numbers of the different kinds of gametes formed. For, if the third type of pairing occurred, we should obtain 4Aa gametes in addition to the 2AA, 4Aa and 2aa derived from the other two types of pairing. The ratio of gametes would then be five containing a dominant to one recessive, there being 1AA : 4Aa : 1aa, as opposed to the ratio 1AA : 2Aa : 1aa obtainable on either of the other modes of segregation.[4] The latter or more usual ratio is the only one considered by Gregory, who apparently takes it for granted that in so far segregation must be of the same sort as in diploid forms.

Let us see which ratio is more in accord with his experimental data. As the ratio of offspring in a back-cross is the same as the gametic ratio, it will be seen that a back-cross of $\frac{A}{a}\frac{A}{a}$ by a recessive should give 3A : 1a plant on Gregory's view, the 3A's consisting of $1\frac{A}{a}\frac{A}{a} : 2\frac{A}{a}\frac{a}{a}$. On the other view, a back-cross should result in 5A : 1a, the 5A's consisting of $1\frac{A}{a}\frac{A}{a} : 4\frac{A}{a}\frac{a}{a}$. On inbreeding an $\frac{A}{a}\frac{A}{a}$ plant, however, owing to the random fertilization of gametes, Gregory's 3 : 1 gametic ratio would result in a 35 : 1 ratio among the offspring (which correspond to F_2) and our own 5 : 1 gametic ratio would give a 35 : 1 ratio of A to a among the offspring.

A summary of his back-crosses of P_1 heterozygous thrum-eyed plants of the type $\frac{A}{a}\frac{A}{a}$ to recessive pin-eyed plants $\frac{a}{a}\frac{a}{a}$ gives the result 61 thrum : 6 pin (10 : 1, as compared to the two expectations 3 : 1 and 5 : 1). Among the F_1 thrums there should

[4] Counts of chromosomes in the maturation divisions of the tetraploid plants show that the chromosomes synapsed in pairs, not in groups of four. Synapsis in fours would be, in effect, the same as pairing of the random sort suggested in this paper, so far as any one set of allelomorphs are concerned, but it might give different linkage results.

on Gregory's view be $1\frac{A}{a}\frac{A}{a}:2\frac{A}{a}\frac{a}{a}$, on the other view $1\frac{A}{a}\frac{A}{a}:4\frac{A}{a}\frac{a}{a}$. Tests of twenty-one F_1 thrums, by mating them to themselves and also to recessives, showed that there was only one which was certainly $\frac{A}{a}\frac{A}{a}$ and 15 which must have been $\frac{A}{a}\frac{a}{a}$. (A few gave numbers too small to be significant, and one or two were of doubtful composition.) This result is within the limits of probable error on the 4:1, but hardly on the 2:1 expectation. The one F_1 thrum plant which was of composition $\frac{A}{a}\frac{A}{a}$ gave, on back-crossing, 67 thrums: 18 pins, a ratio of 3.7:1, to correspond with Gregory's 3:1 or my 5:1 expectation. On inbreeding it gave 44 thrums: 2 pins, a ratio of 22:1, to correspond with Gregory's 15:1 or my 35:1 expectation. The other F_1 thrums, being of composition $\frac{A}{a}\frac{a}{a}$ (aside from the few doubtful ones), gave, on the average, 1 thrum: 1 pin on back-crossing, and 3 thrums: 1 pin on inbreeding; these results would be expected on either view.

Crosses were also made involving the character green versus red stigma (green being dominant). Here the $\frac{A}{a}\frac{A}{a}$ forms, on back-crossing, gave a total of 114 green: 30 red (3.8:1 instead of 3:1 or 5:1), and on inbreeding they gave 75 green: 2 red (37.5:1 instead of 15:1, as on Gregory's expectation, or 35:1, on my own).

It will be seen that the numbers in the above crosses are too small to be very significant, individually, for a settlement of the question at issue, but if summed up they become more decisive. Thus, a summary of the offspring of all back-crosses of the $\frac{A}{a}\frac{A}{a}$ form to the recessive gives 242 dominants (A): 54 recessives (a), or 4.5:1, as compared with the 3:1 expectation of Gregory and the 5:1 of the view advocated in this paper. Where the dominants among these offspring were tested they were found to consist of $1\frac{A}{a}\frac{a}{a}$ and $15\frac{A}{a}\frac{A}{a}$, as compared with the 1:2 expectation of Gregory, and ours of 1:4. Finally, a summary of the cases where $\frac{A}{a}\frac{A}{a}$ forms were inbred shows that 119 dominants: 4 recessives resulted, a ratio of 30:1 where Greg-

ory's expectation would be 15:1 and our own 35:1. Moreover, the individual records fluctuate in both directions about the ratios to be expected upon our point of view, but practically all vary in the same direction from the expectation of Gregory, namely, in the direction of the other expectation.

There is reason, then, to believe that in these *Primulas* the factors derived from the same parents may segregate from each other as allelomorphs, while allelomorphs derived from opposite parents meanwhile assort at random. For although the allelomorphs exist in sets of four they must pair two by two for segregation, as do the chromosomes, and two derived from the same parent may happen to pair with one another. The chance that this should occur is one third, since there are three possible modes of pairing. Such a result is difficult to explain except on the chromosome view of heredity. It would give ratios different from those theoretically expected by Gregory, but more in accord with his experimental data. The principle upon which our own expectation is founded may be briefly summed up by saying that where more than two factors which are normally allelomorphic to each other are present, the pairing of these allelomorphs with each other preparatory to segregation usually[5] takes place at random.

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[5] That this is not always true is shown by Bridges' case of "non-disjunctional" females of *Drosophila,* which contain one Y and two X chromosomes. Any two of these chromosomes normally act as homologues to each other in the reduction division of the normal fly, which contains only two of them. But where all three are present together they do not pair at random, for they oftener undergo the segregation X–XY than XX–Y presumably because the two X's are much more like each other than like the Y, and so more apt to act as homologues.